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CONSERVATION

Diversity and community structure of rapids-dwelling fishes of the Xingu River: Implications for conservation amid large-scale hydroelectric development

Daniel B. Fitzgerald[a,*], Mark H. Sabaj Perez[b], Leandro M. Sousa[c], Alany P. Gonçalves[c], Lucia Rapp Py-Daniel[d], Nathan K. Lujan[e], Jansen Zuanon[d], Kirk O. Winemiller[a], John G. Lundberg[b]

[a] Department of Wildlife and Fisheries Sciences, Applied Biodiversity Science Program, Texas A&M University, College Station, TX 77845, USA
[b] Ichthyology Department, Academy of Natural Sciences of Philadelphia and Drexel University, Philadelphia, PA 19103, USA
[c] Faculdade de Ciências Biológicas, Laboratório de Ictiologia, Universidade Federal do Pará, Altamira, PA, Brazil
[d] Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil
[e] Department of Biological Science, University of Toronto Scarborough, Toronto, ON M1C 1A4, Canada

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ABSTRACT

A recent boom in hydroelectric development in the world's most diverse tropical river basins is currently threatening aquatic biodiversity on an unprecedented scale. Among the most controversial of these projects is the Belo Monte Hydroelectric Complex (BMHC) on the Xingu River, the Amazon's largest clear-water tributary. The design of the BMHC creates three distinctly altered segments: a flooded section upstream of the main dam, a middle section between the dam and the main powerhouse that will be dewatered, and a downstream section subject to flow alteration from powerhouse discharge. This region of the Xingu is notable for an extensive series of rapids known as the Volta Grande that hosts exceptional levels of endemic aquatic biodiversity; yet, patterns of temporal and spatial variation in community composition within this highly threatened habitat are not well documented. We surveyed fish assemblages within rapids in the three segments impacted by the BMHC prior to hydrologic alteration, and tested for differences in assemblage structure between segments and seasons. Fish species richness varied only slightly between segments, but there were significant differences in assemblage structure between segments and seasons. Most of the species thought to be highly dependent on rapids habitat, including several species listed as threatened in Brazil, were either restricted to or much more abundant within the upstream and middle segments. Our analysis identified the middle section of the Volta Grande as critically important for the conservation of this diverse, endemic fish fauna. Additional research is urgently needed to determine dam operations that may optimize energy production with an environmental flow regime that conserves the river's unique habitat and biodiversity.

1. Introduction

Hydrologic alteration of rivers is widespread, with nearly two-thirds of the world's large rivers impacted by dams (Nilsson et al., 2005). Dams represent one of the greatest threats to aquatic biodiversity worldwide (Vörösmarty et al., 2010); their impacts on flow dynamics and river connectivity cause biotic homogenization, promote invasion of exotic species, favor generalist over specialist species, and increase extinction risk for endemic taxa (Johnson et al., 2008; Liermann et al., 2012; Rahel, 2000). Until recently, highly diverse tropical rivers had few large dams (Liermann et al., 2012), but a boom in hydroelectric

development in the world's great tropical river basins is now threatening aquatic biodiversity on an unprecedented scale (Winemiller et al., 2016; Zarfl et al., 2015).

The Amazon Basin holds the highest concentration of aquatic biodiversity on the planet, with 2411 described fish species (roughly 16% of global freshwater fish diversity), at least 1089 endemic species, and ongoing discovery of new species (Reis et al., 2016). Currently, 416 dams are operational or under construction within the basin and an additional 334 have been proposed (Winemiller et al., 2016), which together would leave only three free-flowing Amazon tributaries within the next few decades (Castello and Macedo, 2016; Fearnside, 2006).
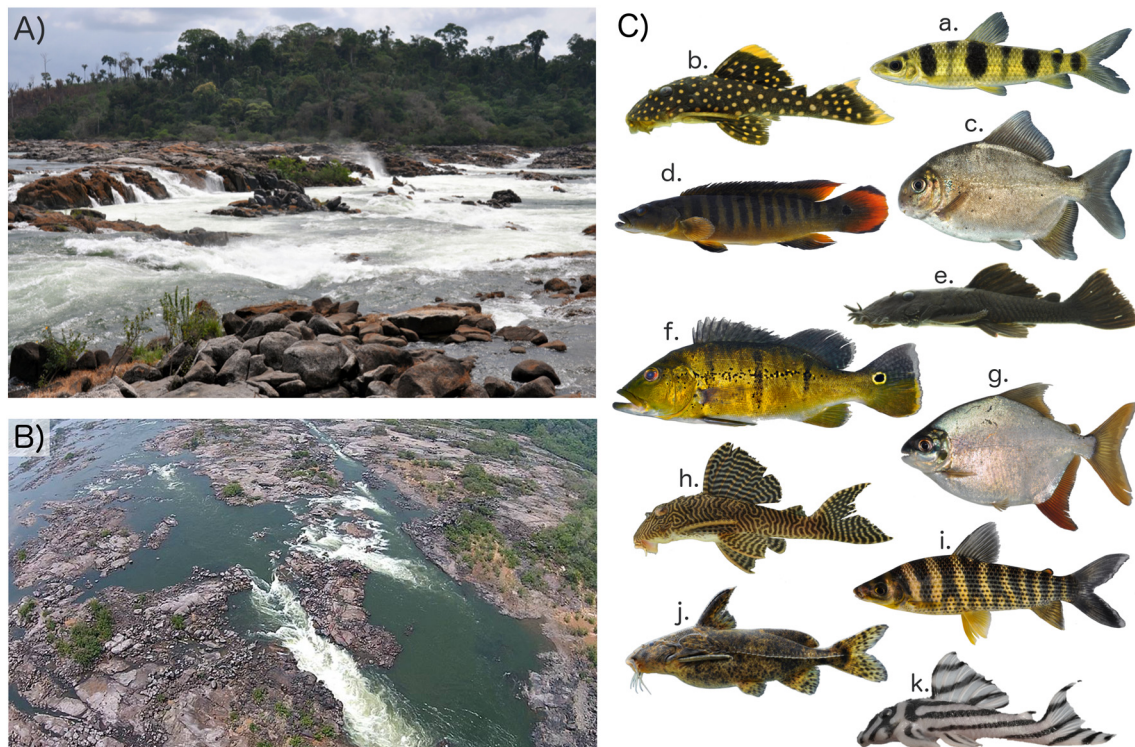
Fig. 1. Examples of the habitat (A, B) and fishes (C) characteristic of the Middle Xingu River. Species shown are: a) *Leporinus maculatus* (Anostomidae), b) *Baryancistrus xanthellus* (Loricariidae), c) *Ossubtus xinguense* (Serrasalmidae), d) *Crenicichla* sp. (Cichlidae), e) *Ancistrus ranunculus* (Loricariidae), f) *Cichla melaniae* (Cichlidae), g) *Tometes kranponhah* (Serrasalmidae), h) *Hypancistrus* sp. (Loricariidae), i) *Leporinus fasciatus* (Anostomidae), j) *Rhinodoras* sp. (Doradidae) and k) *Hypancistrus zebra* (Loricariidae).

Existing dams in the Amazon are concentrated in the Tocantins, Tapajós, Xingu, and other tributaries draining ancient granitic shields, which contain more than twice as many endemic species compared to tributaries draining younger Andean regions (Castello and Macedo, 2016). In addition to the higher concentration of dams in these tributaries, site selection for development projects generally targets areas with high-gradient reaches due to their large hydropower potential. Unfortunately, these same areas often harbor exceptional aquatic diversity.

The Xingu River is the largest clearwater tributary of the Amazon, and contains a unique segment known as the Volta Grande: a 130 km stretch of rapids and anastomosing channels flowing over the crystalline bedrock of the Brazilian Shield (Fig. 1A & B). The river's strong seasonality, steep gradient, and complex geomorphology, with numerous braided channels ranging in width from several meters to several kilometers, create substantial habitat heterogeneity that contributes to the maintenance of a globally unique fish fauna (Fig. 1C). Because the Xingu Basin does not follow a gradual transition from high-gradient to low-gradient conditions (Camargo et al., 2004; Sabaj Pérez, 2015), assemblage structure may be influenced more by discrete barriers such as rapids and waterfalls than gradual changes (Balon and Stewart, 1983; Ibanez et al., 2007; Lujan et al., 2013). Surveys of fish diversity within the basin have identified the Volta Grande as a region of particularly high diversity and endemism (Camargo et al., 2004), though distributional limits of species within the Volta Grande and adjacent reaches remain largely unknown. Recent surveys in this area have collected over 450 species of fishes in 48 families (Sabaj Pérez, 2015), many of which are highly adapted to life within rapids (Zuanon, 1999). Of the 63 species known to be endemic to the Xingu Basin (Winemiller et al., 2016), at least 26 are known only from the large rapids complex in the Volta Grande region (Sabaj Peréz et al., unpublished). Although demographic and distribution data for many species are lacking, and taxonomic descriptions are ongoing, several

species have already been listed as threatened in Brazil (National Red List, 2016), including the critically endangered *Hypancistrus zebra* (zebra pleco; Fig. 1C-k), endangered *Teleocichla centisquama*, and vulnerable *Ossubtus xinguense* (eagle-beaked pacu; Fig. 1C-c).

The same factors that promote the tremendous aquatic diversity of the Xingu's Volta Grande also contribute to the hydropower potential of the region, making the middle Xingu the focus of one of the most controversial development projects in the Amazon: the Belo Monte Hydroelectric Complex (BMHC). A massive engineering project, the BMHC is projected to have an installed capacity of 11,233 MW (3rd largest in the world). Initial proposals in 1975 received considerable backlash due to plans for a series of five separate reservoirs within indigenous territories (Fearnside, 2006). After intense debate, a redesigned proposal emerged in 2002 focusing on only the dams within the Xingu's Volta Grande region (Fearnside, 2006; Sabaj Pérez, 2015). Unlike traditional designs that place the powerhouse at the foot of the dam, the new design would take advantage of a large elevation gradient by diverting water through a series of man-made canals to a powerhouse nearly 90 m below. While the new design reduces the size of the reservoirs on nearby indigenous territories, it has the added impacts of dewatering a significant portion of the Volta Grande between the diversion dam and the main powerhouse and flooding hundreds of square-kilometers of forest. Despite continued controversy, accusations of political corruption, and significant cost overruns (Lees et al., 2016; Sabaj Pérez, 2015), the Brazilian Environmental Authority authorized the operation of the BMHC on November 24, 2015. The reservoirs are currently filled and the facility has been generating power commercially since April 20, 2016. As of publication, eight turbines are currently online and full operation is expected by 2019 (Portal Brasil, 2016).

Direct impacts of river impoundments are well documented and the BMHC will cause significant and predictable changes to aquatic habitat, resulting in three distinctly altered stretches. Upstream of the diversion

dam, slower water velocities within the impounded reach will result in increased sedimentation (Syvitski et al., 2005), turning the heterogeneous rocky substrate characteristic of this region into a homogenous sandy/muddy bottom. Changes in water depth and clarity will alter light penetration, with likely impacts on the availability of benthic resources. Between the diversion dam and the main powerhouse (located 100 km downstream), dewatering of the channel will reduce available aquatic habitat and increase water temperature, leading to lower levels of dissolved oxygen. Flow regulation will reduce seasonal hydrologic variation (Poff et al., 2007), seasonal access to flooded riparian habitats (Graf, 2006), and may alter downstream transport of resources (Syvitski et al., 2005). Downstream of the powerhouse, seasonal variation will also be reduced, with water quality affected by increased erosion from the powerhouse flow and changes in water temperature and dissolved oxygen from reservoir releases.

Limited data on Amazonian aquatic diversity constrains our ability to detect degradation trends and identify conservation priorities (Castello and Macedo, 2016). In particular, fish assemblage structure in tropical clearwater rivers draining ancient granitic shields (e.g., The Tapajós, Tocantins, Ventuari, Xingu) has received little attention compared to other tropical and temperate river types (Lujan and Conway, 2015). Understanding how fish diversity will respond to expected habitat changes requires data on assemblage structure within the impacted area. Despite the rich aquatic diversity of the Xingu's rapids and the long, controversial history of the BMHC, available data on fish assemblage structure within the region are limited to surveys of slack-water habitats and slower areas adjacent to rapids (Barbosa et al., 2015; Schmid et al., 2017). While providing an important characterization of fish assemblages throughout the impacted region, the gillnet surveys used in Barbosa et al. (2015) target a specific microhabitat and are not well suited to sampling benthic fishes in the fastest flowing areas. Because rapids often have distinct fauna that are particularly vulnerable to hydrologic alteration (Lujan and Conway, 2015), data on the structure of these fish assemblages throughout the impacted area are urgently needed. Previous work has explored seasonal variation in functional diversity of fish assemblages within rapids of the Xingu River (Fitzgerald et al., 2017), but no study has analyzed spatial variation in assemblage structure within the rapids.

To address this, we compared the diversity and assemblage structure of fishes in rapids of the Middle and Lower Xingu River prior to hydrologic alteration by the BMHC. Specifically, we ask whether fish diversity and local assemblage structure differ between the three impacted zones (upstream of the diversion dam, middle dewatered section, and downstream of the powerhouse) and how these differences affect conservation and management plans for the river. Because a major impact of river impoundment is reduced seasonal heterogeneity, we further test whether fish assemblage structure in the main channel differs between high- and low-water periods.

2. Methods

2.1. Data collection

A 400-km stretch of the Middle and Lower Xingu River surrounding the area to be impacted by the BMHC was surveyed prior to hydrologic alteration (Fig. 2). Three survey periods were selected to represent multiple stages of an annual hydrologic cycle: September 2013 (low water), March 2014 (high water), and November 2014 (low water, rising). Sampling locations were divided into three groups based on anticipated impacts from the BMHC. The 'upstream' section represents the 130-km stretch upstream of the Pimental diversion dam to the confluence of the Xingu and Iriri Rivers that will experience slower flow velocity and lentic conditions within the new impoundment. The 'middle' section represents the 100-km stretch of the Volta Grande between the Pimental Dam and the Belo Monte powerhouse that will experience greatly reduced flows. The 'downstream' section represents

the 171-km stretch downstream of the Belo Monte powerhouse to the confluence of the Xingu and Amazon Rivers that will receive outflow from the BMHC. The number of sites surveyed within each section during each sampling period is provided in Table A1 in Appendix A. All attempts possible were made to balance the number of sites across sections and survey periods, though the logistics of sampling in various hydrologic conditions resulted in slight differences.

Surveys targeted shallow rapids and deep, swift water over rocky substrates within channels of the principal river course. Water velocity ranged from 0 to 4.4 m/s. Each sampling location received 60–80 min of fishing effort over an area of approximately 100 m^2. Fishes were collected by cast net and by hand by experienced divers who work in the ornamental fish trade. The same two divers sampled all sites, with the exception of sites upstream of Altamira in March 2014, when an alternate diver replaced one of them. To our knowledge, collecting fishes by hand represents a novel sampling approach and provides unique insights into fish assemblage structure within rapids that are difficult to sample with conventional methods. This technique primarily targets benthic species of the family Loricariidae and does not represent the full community of fishes present in the Xingu, though some highly mobile species were also collected. Survey locations and sampling methods used in the present study represent a subset of the total sampling effort of the iXingu Project, which also included surveys of slack-water habitats, littoral zones, floodplain lakes, and tributaries within the study area (Sabaj Pérez et al. unpublished).

2.2. Data analysis

Sample-size based rarefaction/extrapolation curves were used to compare species richness among the three sections. Rarefaction was conducted separately for each survey period following methods developed by Colwell et al. (2012) implemented within the package iNEXT (Chao et al., 2014) using R version 3.2.2 for OS X (R Core Team, 2015). Because taxonomic work in the basin is ongoing (at least 23 new fish species described since 2008), these numbers likely represent conservative estimates of species richness. However, additional analyses that treated easily distinguished morphological variants of some described species (e.g., *Spectracanthicus punctatissimus*, Loricariidae) as distinct taxonomic units produced identical results, suggesting that the major patterns presented should be robust to taxonomic revision.

To compare dominant trends in assemblage structure between sections, we first removed rare species and any species collected at a single site. For the 2013 low-water period, rare species were defined as those with less than 4 individuals, leaving 63 species accounting for 91.5% of fish abundance in samples. Due to lower number of species collected in the remaining two survey periods, rare species were defined as singletons, leaving 51 species accounting for 83.9% of abundance during the 2014 high-water period and 34 species accounting for 89.0% of abundance during the 2014 low-water period.

Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations was used to test for differences in assemblage structure between sections and Non-metric Multidimensional Scaling (NMDS) was used to visualize differences in assemblage structure between sections. NMDS was based on standardized relative abundances fitted to 6 axes; a scree plot was used to select the lowest number of axes without substantial increase in stress, though choice of fewer dimensions produced similar results. Principal Components Analysis was then used to display the two dominant NMDS axes. Euclidean distance between geographic coordinates of sites was used as a starting configuration for the iterative procedure. Finally, a two-way cluster analysis following Ward's D method for hierarchical clustering was used to explore patterns of species composition across sites within each survey period. All community analyses were based on relative abundance data and Bray-Curtis distances, and were performed using the package vegan in R (Oksanen et al., 2015).

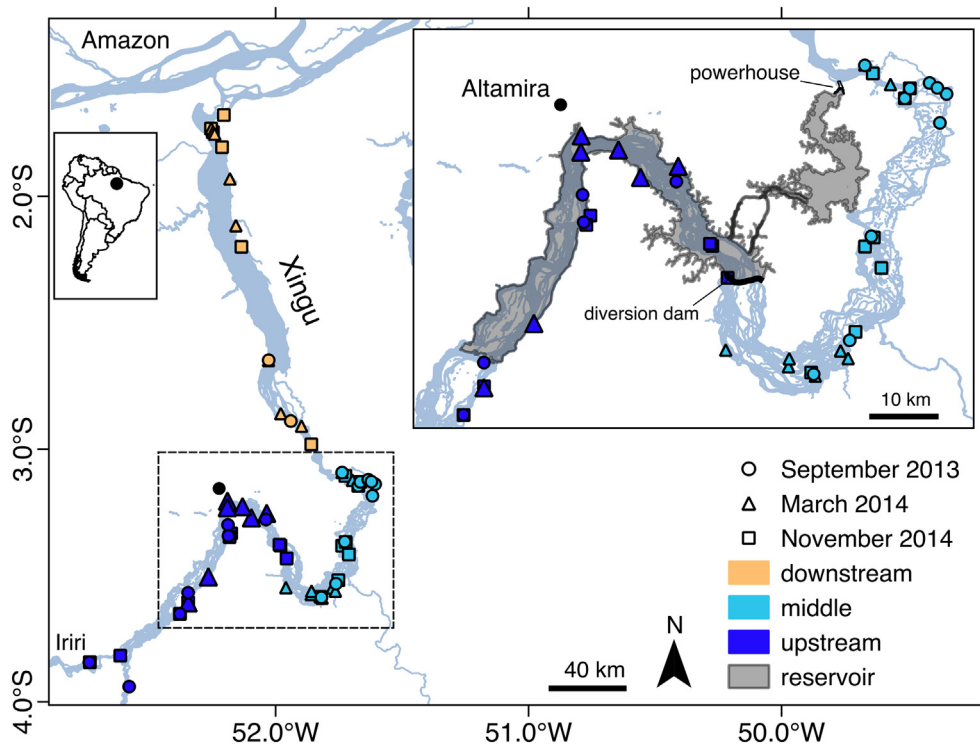To test for differences in species composition during low- and high-

Fig. 2. Map of study region showing sampling locations for three survey periods and three river sections, with area altered by the Belo Monte Hydroelectric Complex shown in inset. Water flow is generally northern.

water periods, the 2013 and 2014 low-water surveys were combined and compared with the 2014 high-water period. Rare species were defined as those with less than 4 individuals in the combined datasets and PERMANOVA and NMDS were performed as described above.

3. Results

A total of 6228 specimens representing 193 species and 23 families was sampled during the three survey periods, with samples dominated by species of the families Loricariidae (41 spp.), Characidae (34 spp.), Cichlidae (26 spp.), Anostomidae (14 spp.), and Doradidae (13 spp.). The upstream, middle, and downstream sections contained 108, 113, and 86 species, respectively. Rarefaction analysis showed that species richness was highest in the upstream section during the 2013 low-water period (Fig. 3A), although 95% confidence intervals of rarefied curves for upstream and downstream sections overlapped during the 2014 low-water period (Fig. 3C). During the 2014 high-water survey, confidence intervals for all sections overlapped (Fig. 3B).

Assemblage structure differed significantly between river sections during all survey periods (PERMANOVA; low water 2013: $F_{(2,23)} = 2.09$, $P = 0.001$; high water 2014: $F_{(2,28)} = 2.00$, $P = 0.001$; low water 2014: $F_{(2,33)} = 2.13$, $P = 0.001$). NMDS revealed partial overlap of the upstream and middle sections and clear separation of the downstream section (Fig. 4). Similarity of the upstream and middle sections was influenced by a core group of species with high relative abundances in both sections that were either absent or present at low relative abundances in the downstream section (Figs. 5, A1–2). This group included *Baryancistrus xanthellus*, *Hypancistrus zebra*, *Scobinancistrus aureatus* (Loricariidae), *Hypomasticus julii*, *Leporinus maculatus*, *Leporellus vitatus* (Anostomidae), *Cichla melaniae* (Cichlidae), and *Corydoras* sp. (Callichthyidae). The distinctness of the upstream section was driven by species such as *Crenicichla percna* (Cichlidae) and *Parancistrus* aff. *aurantiacus* (Loricariidae), whereas species such as *Baryancistrus* sp., *Hopliancistrus* sp. (Loricariidae), *Anostomoides passionis*, and *Pseudanos trimaculatus* (Anostomidae) were only sampled in the

middle section. The middle section was further distinguished from the upstream section by species found at higher relative abundances, such as *Ossubtus xinguense* (Serrasalmidae) and *Ancistrus ranunculus* (Loricariidae).

The clear separation of the downstream section was due to a large group of species only sampled in this section, such as *Crenicichla reticulata*, *Cichla pinima* (Cichlidae), *Hypostomus plecostomus*, *Hypostomus cochliodon* (Loricariidae), *Centrodoras brachiatus*, and *Megalodoras uranoscopus* (Doradidae). Several species were found at sites throughout the study region, such as *Spectracanthicus punctatissimus*, *Spectracanthicus zuanoni*, *Peckoltia vittata*, *Peckoltia sabaji* (Loricariidae), *Geophagus argyrostictus*, *Retroculus xinguensis* (Cichlidae), and *Leporinus fasciatus* (Anostomidae), though relative abundances varied between sections.

Assemblage structure differed significantly between low- and high-water periods (PERMANOVA: $F_{(1,89)} = 1.72$, $P = 0.005$), with 77 species sampled only during low-water surveys and 47 species sampled only during the 2014 high-water survey. In general, species sampled in the main channel under high water conditions were a subset of those found during low-water periods (Fig. A3 in Appendix A). The common loricariids were sampled during both seasons, but several less common species were collected only during low-water periods (e.g., *Baryancistrus* sp., *Acanthicus* sp.) or high water (e.g., *Ancistrus* sp., *Spectracanthicus* sp., *Limatulichthys griseus*). Numerous species of characids, cichlids, and anostomids were sampled only during low-water periods. Most species sampled only at high water were relatively rare, including several species of *Centromochlus* (Auchenipteridae) and *Sternarchorhynchus* (Apteronotidae).

4. Discussion

Species richness was similar between the three sections when all survey periods were combined (Fig. A4 in Appendix A); however, it is important to note that the middle section had similar diversity within a shorter stretch of river. The higher richness observed during low-water
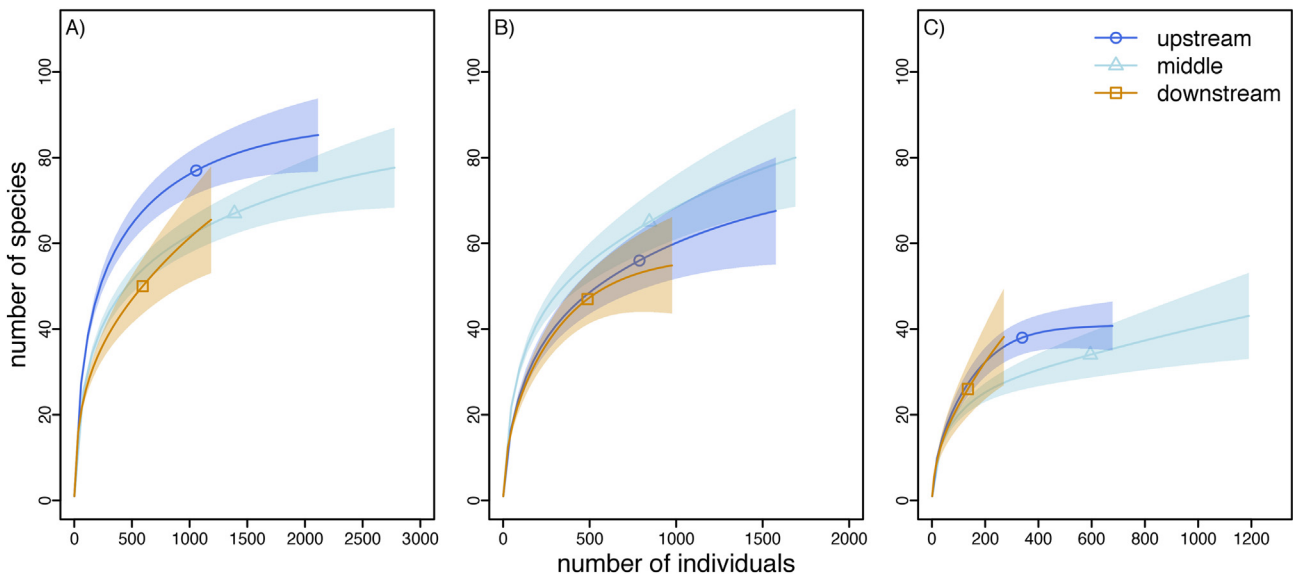
Fig. 3. Rarefaction/extrapolation curves for A) low water September 2013, B) high water March 2014, and C) low water November 2014. Symbols represent actual number of sampled individuals and species for each section. Shaded regions represent 95% confidence intervals for interpolated (left of symbol) and extrapolated (right of symbol) curves.

periods in the upstream section compared to the middle section is likely due to its longer length, which includes the upper half of the highly diverse Volta Grande. The downstream section contained similar species richness as the middle section during all survey periods, despite being roughly 70 km longer. These results further highlight the Volta Grande as a hotspot for fish diversity within the Xingu Basin.

A dominant pattern observed throughout all survey periods is that most species thought to be highly dependent on rapids habitat, including several species listed as threatened in Brazil, were either restricted to or most abundant within the upstream and middle sections. Faunal similarity of these sections was influenced by many shared rheophilic species (Zuanon, 1999), such as *Parancistrus nudiventris* (Rapp Py-Daniel and Zuanon, 2005), *Tometes kranponhah* (Andrade et al., 2016), and the vulnerable *Ossubtus xinguense* (Jegu and Zuanon, 2005). Downstream, many rheophilic species are replaced by species that are more habitat generalists and species common throughout the

Lower Amazon River. Species turnover along fluvial gradients generally corresponds to discontinuities in stream geomorphology and/or abiotic conditions (Jackson et al., 2001; Lujan et al., 2013).

The geomorphology of the upstream and middle sections consists of numerous braided channels and extensive shallow rapids flowing over crystalline bedrock of the Brazilian Shield. Downstream, the Xingu leaves the shield and forms a singular ria-like channel flowing through the alluvial reach of the Lower Amazon River (Sabaj Pérez, 2015; Sioli, 1984). Water velocities in the downstream section remain high, but rocky substrates occur in patches and are deeply submerged. This abrupt transition in river geomorphology likely accounts for the distinct community compositions above and below Belo Monte and may partly explain the high endemism found within the Volta Grande. The same pattern of distinct community structures between the middle and lower Xingu River was found in gill net surveys of slack-water habitats (Barbosa et al., 2015), suggesting that the rapids may serve as a barrier
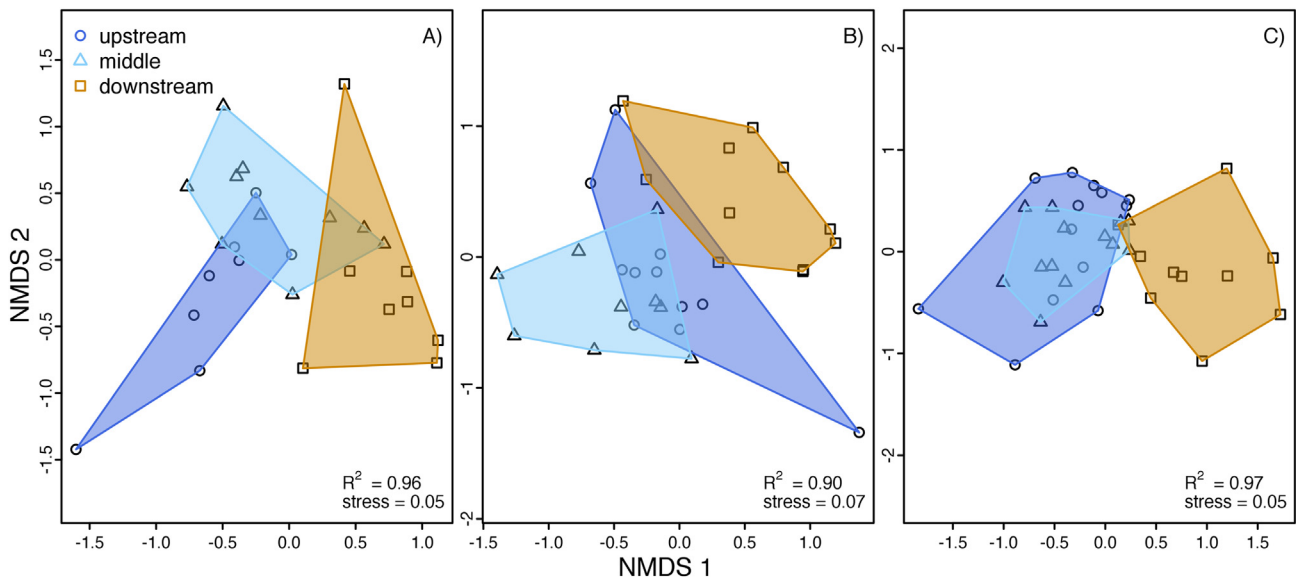

Fig. 4. Non-metric multidimensional scaling results for A) low water September 2013, B) high water March 2014, and C) low water November 2014 based on species relative abundance at sampling sites. Symbols represent sites and shaded polygons are convex hulls for the three river sections.
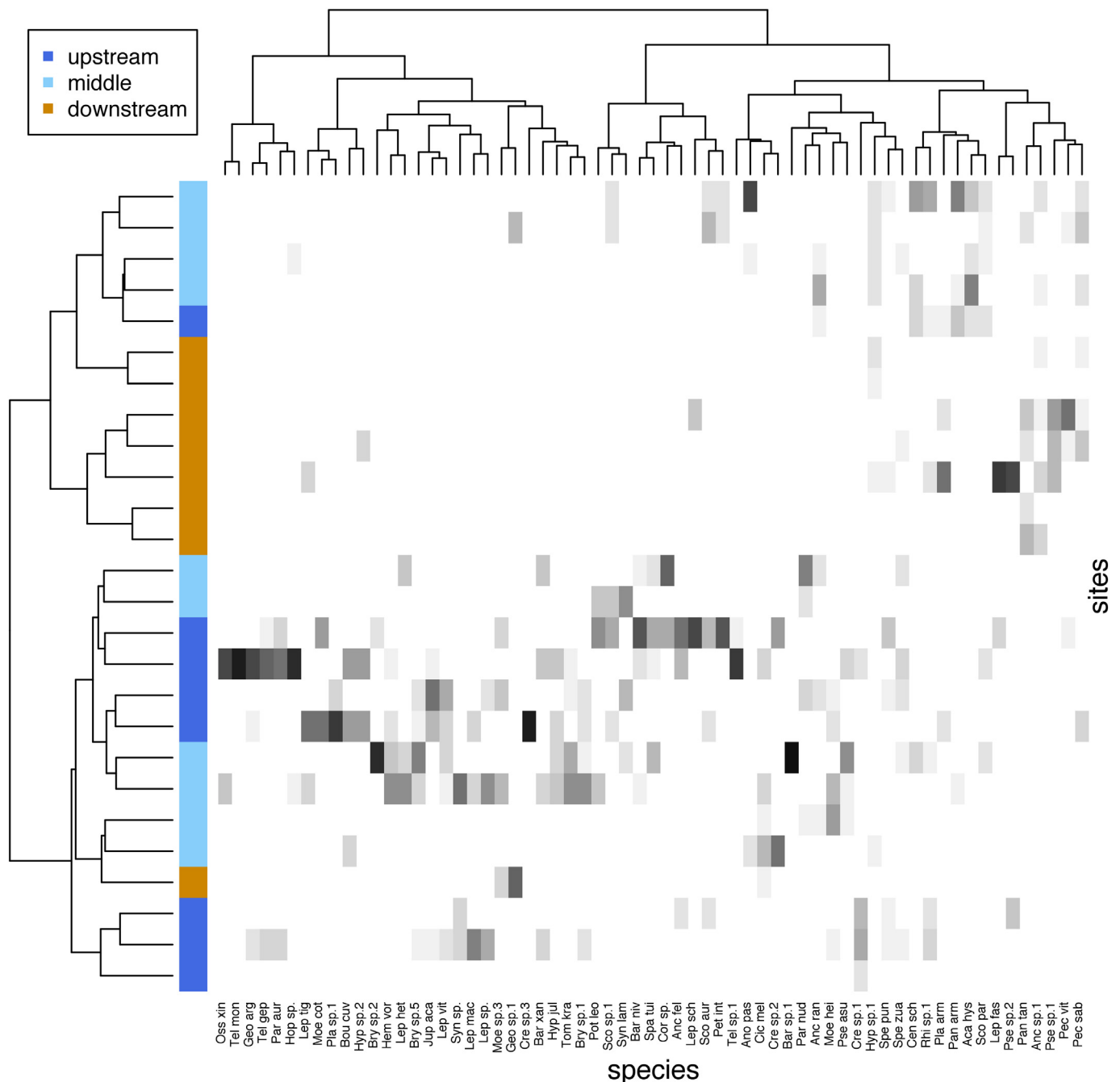
Fig. 5. Two-way cluster analysis of low-water (September 2013) assemblages. Clustering follows Ward's D, using Bray-Curtis dissimilarity matrix based on species relative abundances. Shading along left edge represents river sections and grey-scale shading within represents species relative abundance at a given site ranging from 0 (white) to 1 (black). Species abbreviations and two-way cluster analyses for remaining sampling periods are provided in Appendix A (Table A2 and Figs. A1–2, respectively).

between upland and lowland species for assemblages occupying a range of microhabitats. Unlike other clearwater impoundments where fish assemblage structure was similar throughout the impacted area prior to alteration (Araújo et al., 2013), the distinct community structures found in the present study suggest conservation efforts must carefully consider how differential impacts between segments will affect fish diversity in the region.

Obligate rheophilic species that inhabit shallow rapids in the upstream and middle sections are most susceptible to impacts from hydrologic alteration (Lujan and Conway, 2015). Within the upstream section, the reservoir will eliminate huge areas of rapids habitat. Reduced species richness has been documented following construction of

multiple reservoirs in high-gradient reaches of the clearwater Tocantins River (Araújo et al., 2013; Fearnside, 2001; Lima et al., 2016), as well as other regions of the Amazon (Sá-Oliveira et al., 2015). Reservoirs in both Neotropical and temperate regions often become dominated by a few generalist species (Agostinho et al., 2008; Rahel, 2000). Many rheophilic fishes will likely be extirpated from the upstream section. Soon after formation of the reservoir in 2016, numerous specimens of *Baryancistrus xanthellus* were found dead or dying, with ulcerations and scars, loss of teeth, rotten fins, and sunken body cavities (Adams et al., 2017). Indeed, changes in fish assemblage structure following construction of the Lajeado dam on the Tocantins River were greatest within the reservoir (Araújo et al., 2013). Regional persistence will

depend on both availability of suitable habitat and dispersal ability, which varies widely across taxa. For example, some loricariids (the most diverse and abundant family within the rapids) display local-scale movement, but are generally highly sedentary compared to other fishes, such as certain anostomids and serrasalmids (Lucas and Baras, 2001).

Species unable to disperse will face numerous challenges within the newly impounded upstream section. Habitat complexity has been shown to positively influence freshwater fish diversity by providing enhanced foraging opportunities and lower predation risk (Arrington et al., 2005; Jackson et al., 2001; Schneider and Winemiller, 2008; Willis et al., 2005). Increased sedimentation due to slower water velocities will fill interstitial spaces within structurally complex rocky substrates, reducing opportunities for niche partitioning, refuges from predators, and availability of suitable breeding sites, with likely decreases in local diversity. Several common species inhabiting rapids of the Xingu River are mainly supported by benthic algae (Zuluaga Gómez et al., 2016), with Podostemaceae plants and their associated invertebrate fauna also constituting important food resources for rheophilic species (Flausino Junior et al., 2016). Changes in water depth, clarity, and temperature may alter the availability of resources for algivorous fishes, and disruption of the seasonal flooding cycle will cause the extirpation of Podostemaceae stands in rock outcrops. Studies of Amazonian reservoirs have found that a relatively small number of generalist omnivorous and carnivorous species come to dominate these systems (Sá-Oliveira et al., 2015), making the future of specialist primary consumers in the upstream section uncertain. Indeed, the relative abundance of primary consumers declined dramatically following construction of the Tucuruí reservoir in the neighboring Tocantins River (Fearnside, 2001; Merona et al., 2001) and similar impacts will likely occur in the Xingu. Reduced concentrations of dissolved oxygen at the bottom of the reservoir may place additional metabolic stress on the numerous benthic fishes adapted to the highly oxygenated rapids characteristic of the Xingu. Consistent with these anticipated impacts, Barbosa et al. (2015) found that dissolved oxygen and total suspended matter were among the environmental variables with the greatest influence on fish assemblage structure in slack-water habitats of the middle and lower Xingu.

Species present in the middle section will face a very different set of challenges. Maintenance of aquatic biodiversity requires both base flow to provide sufficient habitat and periodic flow pulses that influence geomorphological dynamics and a host of critical ecological processes. The annual flood pulse is the primary environmental driver of tropical rivers, influencing biotic interactions, access to productive floodplain habitats, and timing of reproductive and migratory patterns (Junk et al., 1989; Lucas and Baras, 2001; Winemiller et al., 2014). Current estimates of the flow that will remain throughout the dewatered section range between 17 and 25% of mean total annual discharge, significantly reducing the wetted area of the channel (see supporting information in Stickler et al., 2013). The Pimental diversion dam will greatly reduce seasonal and inter-annual variation, removing a key component of the system's heterogeneity. Fitzgerald et al. (2017) analyzed seasonal changes in functional diversity of Xingu fish assemblages using a subset of the species analyzed presently, finding patterns consistent with a decreased influence of biotic interactions during the high-water period. This seasonal variation in community assembly dynamics likely plays a role in maintaining diversity. Reduced seasonal dynamics in the dewatered portion and greater competition for remaining aquatic space year-round may lead to both reduction of diversity due to competitive displacement and significant changes in community structure. Species that rely on flooded riparian forests will lack access to vital resources, such as terrestrial food subsidies and seasonal breeding sites. The seasonal differences in community structure observed in this study may be partly explained by differences in sampling efficiency, but the absence of many anostomids, characids, and serrasalmids from main channel habitats during the wet season could also have been due to their lateral migrations into flooded habitats (Lucas and Baras, 2001).

In addition, the combination of reduced flow and the Pimental impoundment will greatly reduce the ability of longitudinal migrants to navigate the channel. Fish ladders have been installed at Pimental, but these have proven ineffective as a mitigation strategy for other Neotropical impoundments (Pompeu et al., 2012) and will not aid species trying to navigate the dewatered rapids and waterfalls of the lower Volta Grande.

Fishes inhabiting deep rocky areas of the downstream section tended to be wide-ranging and environmentally tolerant; however, several rapids-associated species also were present in this section. The outflow from the main powerhouse will maintain sufficient discharge, though the attenuated seasonal variability will create similar impacts to those discussed above. In addition, changes in thermal profile, oxygen content, and nutrient levels due to reservoir releases may disproportionately affect clear-water species with narrow environmental tolerances, shifting community structure towards an even greater influence of lowland Amazonian species and resulting in reduction of Beta diversity.

The presence of such a unique assemblage of rapids-adapted species in the upstream and middle sections, including the critically endangered *Hypancistrus zebra* and other threatened species, clearly highlights these stretches as conservation priorities. Because the instream reservoir is necessary for the hydropower potential of the BMHC, there is little that can be done for the conservation of rapids habitats in the upstream section. In fact, the two reservoirs currently built are projected to generate only a fraction of the full BMHC capacity, leaving many to speculate that developers will leverage this to build additional impoundments further upstream as originally proposed (Fearnside, 2006; Stickler et al., 2013). This pressure will only increase given the projected decline in discharge for the Xingu due to continued deforestation in the region (Stickler et al., 2013) and to uncertainties regarding future precipitation patterns in the eastern Amazon (Sorribas et al., 2016). While conservation efforts should continue to resist development of additional dams upstream, it is clear that conserving fish diversity and endemism currently found throughout the study reach will depend critically on how the dewatered portion (i.e., middle section in our study) of the Volta Grande is managed.

Allowing for a dynamic flow regime will be critical to maintaining diversity within the dewatered section. Average monthly discharge in the Xingu River near Altamira ranged from 1110 to 20,617 m^3/s during the period 1971–2015, with peak high-water discharges ranging from 9861 to 30,112 m^3/s (HidroWeb, 2015). Ideally, releases from the Pimental impoundment would mimic not only the seasonal dynamic, but incorporate the over 20,000 m^3/s of inter-annual variability observed in peak high-water discharge. The sustainability boundaries approach to determining environmental flows (Richter, 2009), in which requirements are expressed as allowable percentages of deviation rather than particular volumes at given times of year, would aid in maintaining flow dynamics throughout the lower Volta Grande and lower Xingu. Determining appropriate boundaries is a difficult process that is beyond the scope of this paper, but the roughly 80% reduction currently expected will likely leave insufficient flows for the maintenance of aquatic diversity.

Protection from further disruption in the dewatered area will be essential. The Canadian mining company Belo Sun has been granted a 1305 km^2 concession to build Brazil's largest gold mine in the dewatered channel, immediately downstream of the Pimental diversion dam (Lees et al., 2016). Draft legislation allowing mining operations in protected areas and indigenous lands in Brazil (Mining Code Bills 37/2011, 3682/2012, and 1610/96) will open the doors to further expansion within the adjacent Paquiçamba and Arara Indigenous territories. Gold mining has had significant effects on water quality, biodiversity, and environmental/human health along other Amazonian rivers (Swenson et al., 2011), and efforts are needed to prevent such developments within the dewatered stretch of the Volta Grande.

Continued environmental monitoring will be needed to manage

aquatic biodiversity post hydrologic-alteration. Monitoring efforts for fishes are in place (Barbosa et al., 2015), but should be expanded to include additional components of aquatic biodiversity, riparian forest cover, and impacts on local livelihoods. In addition, non-invasive monitoring approaches should be explored and implemented where possible (Schmid et al., 2017). Captive breeding programs have been initiated for several species of conservation concern, including the critically endangered *Hypancistrus zebra* (zebra pleco); however, these strategies do little to promote conservation of critical habitat for remaining species. While hydrological methods for determining flow downstream of the diversion dam can be used initially, studies on habitat requirements of target species or assemblages will be necessary for more sophisticated habitat simulation or holistic approaches for generating optimum flow recommendations in the future (Tharme, 2003).

The middle Xingu has been described as a river of rivers (Sabaj Pérez, 2015), where channels approximating the geomorphology of small streams are interwoven with those of more typical higher-order channels. Undoubtedly, this complexity is partly responsible for the aquatic diversity currently found there, making it imperative to maintain the variety and amount of flow necessary to sustain this globally unique habitat throughout the remainder of the Volta Grande.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.04.002.

References

Adams, C., Sawakuchi, A.O., Zuanon, J., Cunha, J.M., Salm, R., Carneiro, C.C., Francesco, A., Rodrigues, R.R., Pereira, T.S., 2017. Situação ambiental no trecho do rio Xingu afetado pela UHE Belo Monte a montante da barragem Pimental. In: Magalhães, S.B., Cunha, M.C. (Eds.), A expulsão de ribeirinhos em Belo Monte. SBPC, São Paulo, pp. 129–150.

Agostinho, A.A., Pelicice, F.M., Gomes, L.C., 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz. J. Biol. 68, 1119–1132.

Andrade, M.C., Jegu, M., Giarrizzo, T., 2016. *Tometes kranponhah* and *Tometes ancylorhynchus* (Characiformes: Serrasalmidae), two new phytophagous serrasalmids, and the first *Tometes* species described from the Brazilian Shield. J. Fish Biol. 89, 467–494.

Araújo, E.S., Marques, E.E., Freitas, I.S., Neuberger, A.L., Fernandes, R., Pelicice, F.M., 2013. Changes in distance decay relationships after river regulation: similarity among fish assemblages in a large Amazonian river. Ecol. Freshw. Fish 22, 543–552.

Arrington, D.A., Winemiller, K.O., Layman, C.A., 2005. Community assembly at the patch scale in a species rich tropical river. Oecologia 144, 157–167.

Balon, E.K., Stewart, D.J., 1983. Fish assemblages in a river with unusual gradient (Luongo, Africa-Zaire system), reflections on river zonation and description of another new species. Environ. Biol. Fish 9, 225–252.

Barbosa, T.A., Benone, N.L., Begot, T.O., Goncalves, A., Sousa, L., Giarrizzo, T., Juen, L., Montag, L., 2015. Effect of waterfalls and the flood pulse on the structure of fish assemblages of the middle Xingu River in the eastern Amazon basin. Braz. J. Biol. 75, 78–94.

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.

Castello, L., Macedo, M.N., 2016. Large-scale degradation of Amazonian freshwater ecosystems. Glob. Chang. Biol. 22, 990–1007.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., Longino, J.T.,

2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J. Plant Ecol. 5, 3–21.

Fearnside, P.M., 2001. Environmental impacts of Brazil's Tucuruí Dam: unlearned lessons for hydroelectric development in Amazonia. Environ. Manag. 27, 377–396.

Fearnside, P.M., 2006. Dams in the Amazon: Belo Monte and Brazil's hydroelectric development of the Xingu River basin. Environ. Manag. 38, 16–27.

Fitzgerald, D.B., Winemiller, K.O., Sabaj Pérez, M.H., Sousa, L.M., 2017. Seasonal changes in the assembly mechanisms structuring tropical fish communities. Ecology 98, 21–31.

Flausino Junior, N., Machado, F.A., Zuanon, J.S., Ferreira, E.J., 2016. The fish fauna of sessile hydrophyte stands (*Mourera* spp.: Podostemaceae) in the Dardanelos waterfalls, Rio Aripuanã, Brazil. Aqua 22, 133–144.

Graf, W.L., 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology 79, 336–360.

HidroWeb, 2015. Sistema de Informações Hidrológicas. Agencia Nacional de Águas, Brazil. http://www.snirh.gov.br/hidroweb, Accessed date: 13 December 2016.

Ibanez, C., Oberdorff, T., Teugels, G., Mamononekene, V., Lavoué, S., Fermon, Y., Paugy, D., Toham, A.K., 2007. Fish assemblages structure and function along environmental gradients in rivers of Gabon (Africa). Ecol. Freshw. Fish 16, 315–334.

Jackson, D.A., Peres-Neto, P.R., Olden, J.D., 2001. What controls who is where in freshwater fish communities — the roles of biotic, abiotic, and spatial factors. Can. J. Fish. Aquat. Sci. 58, 157–170.

Jegu, M., Zuanon, J., 2005. Threatened fishes of the world: *Ossubtus xinguense* (Jegu 1992) (Characidae: Serrasalminae). Environ. Biol. Fish 73, 414.

Johnson, P.T.J., Olden, J.D., vander Zanden, M.J., 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. Front. Ecol. Environ. 6, 359–365.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. In: Dogde, D.P. (Ed.), Proceedings of the International Large Rivers Symposium, Ottawa, pp. 110–127.

Lees, A.C., Peres, C.A., Fearnside, P.M., Schneider, M., Zuanon, J.A.S., 2016. Hydropower and the future of Amazonian biodiversity. Biodivers. Conserv. 25, 451–466.

Liermann, C.R., Nilsson, C., Robertson, J., Ng, R.Y., 2012. Implications of dam obstruction for global freshwater fish diversity. Bioscience 62, 539–548.

Lima, A.C., Agostinho, C.S., Sayanda, D., Pelicice, F.M., Soares, A.M.V.M., Monaghan, K.A., 2016. The rise and fall of fish diversity in a neotropical river after impoundment. Hydrobiologia 763, 207–221.

Lucas, M.C., Baras, E., 2001. Migration of Freshwater Fishes. Blackwell Science, Oxford, UK.

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

Lujan, N.K., Roach, K.A., Jacobsen, D., Winemiller, K.O., Vargas, V.M., Ching, V.R., Maestre, J.A., 2013. Aquatic community structure across an Andes-to-Amazon fluvial gradient. J. Biogeogr. 40, 1715–1728.

Merona, B., dos Santos, G.M., de Almeida, R.G., 2001. Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. Environ. Biol. Fish 60, 375–392.

National Red List, 2016. Brazilian Red List. http://www.nationalredlist.org (accessed 24 June 2016).

Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science 308, 405–408.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2015. vegan: Community Ecology Package. R Package, Version 2.3-1. https://cran.r-project.org/web/packages/vegan/index.html, Accessed date: 25 September 2015.

Poff, N.L., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proc. Natl. Acad. Sci. U. S. A. 104, 5732–5737.

Pompeu, P.S., Agostinho, A.A., Pelicice, F.M., 2012. Existing and future challenges: the concept of successful fish passage in South America. River Res. Appl. 28, 504–512.

Portal Brasil, 2016. Dilma inaugura usina hidrelétrica de Belo Monte. http://www.brasil.gov.br/governo/2016/05/dilma-inaugura-usina-hidreletrica-de-belo-monte, Accessed date: 25 May 2016.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. http://www.r-project.org, Accessed date: 25 September 2015.

Rahel, F.J., 2000. Homogenization of fish faunas across the United States. Science 288, 854–856.

Rapp Py-Daniel, L.H., Zuanon, J., 2005. Description of a new species of *Parancistrus* (Siluriformes: Loricariidae) from the rio Xingu, Brazil. Neotropical Ichthyol. 3, 571–577.

Reis, R.E., Albert, J.S., Di Dario, F., Mincarone, M.M., Petry, P., Rocha, L.A., 2016. Fish biodiversity and conservation in South America. J. Fish Biol. 89, 12–47.

Richter, B.D., 2009. Re-thinking environmental flows: from allocations and reserves to sustainability boundaries. River Res. Appl. 26, 1052–1063.

Sabaj Pérez, M.H., 2015. Where the Xingu bends and will soon break. Am. Sci. 103, 395–403.

Sá-Oliveira, J.C., Hawes, J.E., Isaac-Nahum, V.J., Peres, C.A., 2015. Upstream and downstream responses of fish assemblages to an eastern Amazonian hydroelectric dam. Freshw. Biol. 60, 2037–2050.

Schmid, K., Reis-Filho, J.A., Harvey, E., Giarrizzo, T., 2017. Baited remote underwater video as a promising nondestructive tool to assess fish assemblages in clearwater Amazonian rivers: testing the effect of bait and habitat type. Hydrobiologia 784, 93–109.

Schneider, K.N., Winemiller, K.O., 2008. Structural complexity of woody debris patches influences fish and macroinvertebrate species richness in a temperate floodplain-river system. Hydrobiologia 610, 235–244.

Sioli, H., 1984. The Amazon and its main affluents: hydrography, morphology of the river courses and river types. In: Sioli, H. (Ed.), The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin. Springer Netherlands, Dordrecht, pp. 127–165.

Sorribas, M.V., Paiva, R.C.D., Melack, J.M., Bravo, J.M., Jones, C., Carvalho, L., Beighley, E., Forsberg, B., Costa, M.H., 2016. Projections of climate change effects on discharge and inundation in the Amazon basin. Climate Change 136, 555–570.

Stickler, C.M., Coe, M.T., Costa, M.H., Nepstad, D.C., McGrath, D.G., Dias, L.C.P., Rodrigues, H.O., Soares-Filho, B.S., 2013. Dependence of hydropower energy generation on forests in the Amazon Basin at local and regional scales. Proc. Natl. Acad. Sci. U. S. A. 110, 9601–9606.

Swenson, J.J., Carter, C.E., Domec, J.C., Delgado, C.I., 2011. Gold mining in the Peruvian Amazon: global prices, deforestation, and mercury imports. PLoS One 6, e18875.

Syvitski, J.P.M., Vörösmarty, C.J., Kettner, A.J., Green, P., 2005. Impact of humans on the flux of terrestrial sediment to the global coastal ocean. Science 308, 376–380.

Tharme, R.E., 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. River Res. Appl. 19, 397–441.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561.

Willis, S.C., Winemiller, K.O., Lopez-Fernandez, H., 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142, 284–295.

Winemiller, K.O., Montana, C.G., Roelke, D.L., Cotner, J.B., Montoya, J.V., Sanchez, L., Castillo, M.M., Layman, C.A., 2014. Pulsing hydrology determines top-down control of basal resources in a tropical river-floodplain ecosystem. Ecol. Monogr. 84, 621–635.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I.G., Darwall, W., Lujan, N.K., Harrison, I., Stiassny, M.L.J., Silvano, R.A.M., Fitzgerald, D.B., Pelicice, F.M., Agostinho, A.A., Gomes, L.C., Albert, J.S., Baran, E., Petrere, M., Zarfl, C., Mulligan, M., Sullivan, J.P., Arantes, C.C., Sousa, L.M., Koning, A.A., Hoeinghaus, D.J., Sabaj Pérez, M.H., Lundberg, J.G., Armbruster, J., Thieme, M.L., Petry, P., Zuanon, J., Torrente Vilara, G., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C.S., Akama, A., Van Soesbergen, A., Sáenz, L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351, 128–129.

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., Tockner, K., 2015. A global boom in hydropower dam construction. Aquat. Sci. 77, 161–170.

Zuanon, J., 1999. História natural da ictiofauna de corredeiras do rio Xingu, na região de Altamira, Pará, In Instituto de Biologia. Universidade Estadual de Campinas, Campinas, SP, Brazil, pp. 198.

Zuluaga Gómez, M.A., Fitzgerald, D.B., Giarrizzo, T., Winemiller, K.O., 2016. Morphologic and trophic diversity of fish assemblages in rapids of the Xingu River, a major Amazon tributary and region of endemism. Environ. Biol. Fish 99, 647–658.