UNIVERSIDADE FEDERAL DE LAVRAS

MARINA FERREIRA MOREIRA

O PAPEL DE RIBEIRÕES PARA A MANUTENÇÃO DA DIVERSIDADE DE PEIXES NO ALTO SÃO FRANCISCO

LAVRAS – MG

2022

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestra.

Prof. Dr. Paulo dos Santos Pompeu
Orientador

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MARINA FERREIRA MOREIRA

O PAPEL DE RIBEIRÕES PARA A MANUTENÇÃO DA DIVERSIDADE DE PEIXES NO ALTO SÃO FRANCISCO

THE ROLE OF INTERMEDIATE SIZE RIVERS IN MAINTENANCE OF FISH DIVERSITY IN ALTO SÃO FRANCISCO

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestra.

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Dr. Daniel de Melo Rosa, Universidade Federal de Lavras

Prof. Dr. Paulo dos Santos Pompeu

Orientador

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"Somos o resultado de tanta gente, de tanta história, tão grandes sonhos que vão passando de pessoa a pessoa, que nunca estaremos sós."
(Valter Hugo Mãe)

Fazer um mestrado inteiro durante uma pandemia está entre os maiores desafios que já enfrentei. Entre mudar o meu projeto de pesquisa, a insegurança de viajar para as coletas e escrever a dissertação enquanto eu estava com covid... eu consegui. Mas essa etapa só foi concluída porque eu estava cercada de pessoas incríveis durante todo esse processo.

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RESUMO

Na região tropical, entre os ecossistemas lóticos de água doce, os rios de médio porte são pouco conhecidos, em relação aos rios de cabeceiras e os de grande porte. Eles parecem desempenhar um papel crucial no ciclo de vida dos peixes migradores e possivelmente abrigam uma parte importante da comunidade de peixes da bacia em que estão inseridos. No entanto, poucos estudos investigaram estas questões para diferentes tamanhos de rios e existe uma ausência de publicações mais recentes. Portanto, esse estudo teve como objetivo avaliar se o tamanho do rio influencia os juvenis de espécies migradoras (capítulo um) e os padrões de diversidade (diversidades alfa e beta) da região ao longo de rios de diferentes portes (capítulo dois). Foram analisadas comunidades de peixes de 16 e 48 rios para os capítulos um e dois, respectivamente, na Bacia do Alto São Francisco. Os resultados demonstraram que rios menores, principalmente quando drenam regiões próximas às planícies de inundação, parecem ser os primeiros locais onde os juvenis de espécies migradoras se deslocam após deixarem as lagoas marginais. Também foram levantadas informações indicando que os indivíduos se deslocam gradualmente em direção a rios maiores à medida em que crescem. Os rios analisados apresentaram altos valores de diversidades alfa e beta, sendo o turnover o principal processo que leva a variação de espécies entre os rios de todos os portes. A diversidade alfa aumentou com o tamanho do rio enquanto a diversidade beta não parece ter um padrão claro relacionado a este. Também foram adicionadas 34 espécies de trechos lóticos que ainda não haviam sido registradas para esta região e foi indicado que várias espécies ainda podem ser registradas. O presente trabalho concluiu que os que rios de médio porte, apesar de pouco estudados, são essenciais na manutenção da biodiversidade de toda a bacia, inclusive para espécies de grande porte, como as migradoras.

Palavras-chave: Bacia do São Francisco. Conservação de peixes. Peixe de água doce. Peixes juvenis. Peixes migradores. Tamanho do rio.

ABSTRACT

In the tropical region, among the lotic freshwater ecosystems, the intermediate-sized rivers are little known compared to headwaters and large rivers. They seem to play a crucial role in the life cycle of migratory fishes and possibly harbor an important part of the fish community in their basin. However, few studies have investigated these matters for different river sizes and recent publications are absent. Therefore, this study aimed to assess if the river size influences the juveniles of migratory species (chapter one) and the diversity patterns (alpha and beta diversities) of the region along rivers of different sizes (chapter two). Fish communities from 16 and 48 rivers were analyzed for chapters one and two, respectively, in the upper São Francisco River basin. The results showed that smaller rivers, especially when draining regions close to floodplains, seem to be the first places where juveniles of migratory species move after leaving the floodplain lagoons. Information indicating that individuals gradually move towards larger rivers as they grow were also raised. The analyzed rivers showed high values for alpha and beta diversities, with turnover being the main process leading to species variation among the rivers of all sizes. The alpha diversity showed an increase with the size of the river while the beta diversity does not seem to have a clear pattern related to the river size. 34 additional species from lotic stretches that had not been registered yet for this region were added and it was shown that several additional species can still be recorded. This study concluded that intermediate-sized rivers, despite little studied, are essential in maintaining biodiversity of the entire basin, including for large species, such as migratory.

Key words: fish conservation; freshwater fish; migratory fish; river size; juvenile fish; São Francisco basin.

SUMÁRIO

PRIMEIRA PARTE

INTRODUÇÃO GERAL

1 INTRODUÇÃO GERAL

Na região tropical, dentre os ecossistemas lóticos de água doce, ou seja, aqueles de fluxo de água constante, os cursos d'água de pequeno e grande porte são relativamente bem conhecidos. Nestes primeiros, os estudos focam principalmente na composição da ictiofauna e nos efeitos dos diferentes usos do solo sobre esta (LORION & KENNEDY, 2009; LEAL *et al.*, 2014; CASATTI *et al*., 2015; ZENI *et al.*, 2019), enquanto os trabalhos nos rios de grande porte estão, em maior parte, relacionados aos empreendimentos hidrelétricos instalados nestes, focando nos impactos dos barramentos (AGOSTINHO *et al.*, 2008; DUGAN *et al.*, 2010; LOURES E POMPEU, 2018; SUZUKI *et al*., 2017).

Os rios de médio porte, aqueles entre terceira e quinta ordem (sensu Strahler), conhecidos como ribeirões, são pouco estudados. Parecem exercer um papel crucial no ciclo de vida das espécies de peixes migradores, agindo como área de desenvolvimento de juvenis destas (GODINHO E POMPEU, 2003) e, possivelmente, abrigam parte importante da comunidade de peixes de sua bacia, incluindo espécies características de rios grandes e pequenos. No entanto, poucos estudos investigaram estas questões para diferentes tamanhos de rios (BISTONI E HUED, 2002; WHITESIDE E MCNATT, 1972). Portanto, meu estudo teve como objetivo avaliar se o tamanho do rio influencia os juvenis de espécies migradoras (capítulo um) e os padrões de diversidade (diversidades alfa e beta) de uma bacia hidrográfica, investigando rios de diferentes portes (capítulo dois).

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SEGUNDA PARTE

ARTIGOS

ARTIGO 1

SMALL RIVERS, GREAT IMPORTANCE: REFUGE AND GROWTH SITES OF JUVENILE MIGRATORY FISHES

Artigo redigido conforme as normas da revista Ecology of Freshwater Fish.

Small rivers, great importance: refuge and growth sites of juvenile migratory fishes

Marina F. Moreira[1]; Alexandre Peressin[1]; Paulo S. Pompeu[1]

[1]Laboratório de Ecologia de Peixes, Programa de Pós-Graduação em Ecologia Aplicada, Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras – UFLA, Campus Universitário, 37200-900, Lavras, Minas Gerais, Brasil.

Running title

Small rivers as refuge and growth sites of migratory fishes

Abstract

In South America, the adult life cycle of freshwater migratory fishes is relatively well known. Although several studies have already been conducted on migratory fishes, they are mostly focused on reproductive migration, while sites of growth and refuge of juvenile migratory fish remain poorly investigated. Therefore, we aimed to evaluate the role of smaller rivers in the life cycle of migratory fishes. In particular, we investigated how the size of a river and its location in a basin influence the richness, abundance, and size structure of migratory fish communities. We used the upper São Francisco Basin for this assessment. We selected 16 rivers of different sizes distributed along the entire basin. Each river was sampled once, and fish were captured using a cast net. We found that smaller rivers are important environments in the life cycle of migratory species. These environments, especially when draining regions close to floodplains, seem to be the first places where juveniles of migratory species move after leaving floodplain lagoons. We also obtained information indicating that individuals gradually move towards larger rivers as they grow. Currently, the best known strategy for the conservation of neotropical migratory fishes is the maintenance of free-flowing stretches encompassing necessary habitats for life cycle completion. Here, we conclude that it is also necessary to include the small tributaries of the main channel in these protected free-flowing stretches.

Keywords: fish conservation; fish life cycle; fish migration; floodplain; juvenile fishes; neotropical rivers.

INTRODUCTION

Potamodromous migratory fishes are those that move periodically to complete the stages of their life cycle in different locations within a river basin (Northcote, 1984a; Lucas et al., 2001a). In South America, they are usually large and abundant species and, therefore, of great relevance in commercial fishing (Carosfeld et al., 2003). Despite representing only a small portion of the biodiversity of rivers (approximately 8% in the São Francisco Basin) (Sato & Godinho, 2003), by constituting a large part of the biomass in Neotropical rivers, they significantly contribute to the structuring of communities and ecosystem services. Some of the species are important top predators (Sih et al., 1985), and others are detritivores, acting in nutrient cycling (Flecker, 1996).

In South America, potamodromous fishes from the Paraná and São Francisco Basins have relatively well-known life cycle. During the dry period, individuals remain downstream of the river, where they feed and accumulate energy for the migratory event. With the beginning of the rainy season, just before the river level rises, the individuals swim upstream towards the most favourable areas for spawning. Spawning occurs during flood pulses, and eggs and larvae passively drift towards the floodplains. In these places, they find ideal conditions for their initial development, such as high availability of food resources and shelter from predators. During the next flood pulse, juvenile fishes leave the floodplain lagoons and return to the rivers (Northcote, 1984b; Welcomme, 1985; Carosfeld & Harvey, 2004).

In comparison to other areas within a basin, floodplains have higher primary productivity, which leads to a high availability of food for fish such as zooplankton and phytoplankton, high temperatures and an abundance of refuges provided by macrophytes (Agostinho et al., 2004; Godinho & Godinho, 2003b; Meschiatti et al., 2000), making these areas very suitable sites for larval growth. However, the abundance of predators is also high and is composed mainly of the well-known and voracious carnivorous piranhas (*Pygocentrus* spp. and *Serrasalmus* spp.) (Carvalho et al., 2007) and other species of carnivorous fishes (Meschiatti, Arcifa, & Fenerich-Verani, 2000). Therefore, we think that immediately after the larval phase and at the beginning of the growth and juvenile phases, these fish may leave lagoons and find refuge at other places. It has been suggested that juvenile fishes, after abandoning floodplains, use intermediate-sized rivers as growing sites to avoid predation (Godinho & Pompeu, 2003).

Although several studies have already been conducted on different aspects of the migratory cycle of fish species in the São Francisco River Basin (Arantes et al., 2010; Godinho & Kynard, 2006; Hatanaka et al., 2006; Arantes et al., 2011; Sato et al., 2005), they have generally focused on adult fishes, especially reproductive migration, while growth and refuge sites of juveniles remain poorly investigated. The upper São Francisco Basin is particularly suitable for such assessment. From its headwaters to the Três Marias reservoir, São Francisco is a 400 km free-flowing river. Migratory movements have been described in detail for the region, and spawning sites, feeding areas, and floodplain lagoons distributions are well known (Lopes et al., 2018; Lopes et al., 2019).

Therefore, we aimed to evaluate the role of intermediate sized rivers in the life cycle of migratory fish. In particular, we investigated how the size of the river and its location in the basin influence the richness, abundance, and size structure of the migratory fish communities. We hypothesize that smaller rivers, although harbouring lower species richness, will present smaller and more abundant migratory fish. Moreover, if predation drives juvenile movements into smaller rivers, then the closer a river is to floodplains, the higher their abundance.

MATERIALS AND METHODS

Study area

The study was carried out in the upper São Francisco River Basin, Minas Gerais, Brazil, upstream from the Três Marias reservoir (Figure 1). The Três Marias dam is 75 metres high, and the reservoir flood area can reach up to 1.050 km^2 (Sampaio & López, 2003).

The main river stretch upstream of the reservoir is a 400 km long free-flowing river and extends to São Francisco River springs. Two tributaries, the Samburá and the Bambuí rivers, have been considered the main spawning sites for migratory species (Lopes et al., 2019) and the middle segment of this stretch is considered a nursery area for ichthyofauna because of the presence of floodplains. It contains several floodplain lagoons, perennial and seasonal, both in São Francisco itself and its tributaries, notably the Bambuí river (Sato, Cardoso, & Amorim, 1988; Lopes et al., 2019).

This area has a well-marked period of drought and rain, which occurs from June to October and from November to February, respectively (Sato & Godinho, 2003).

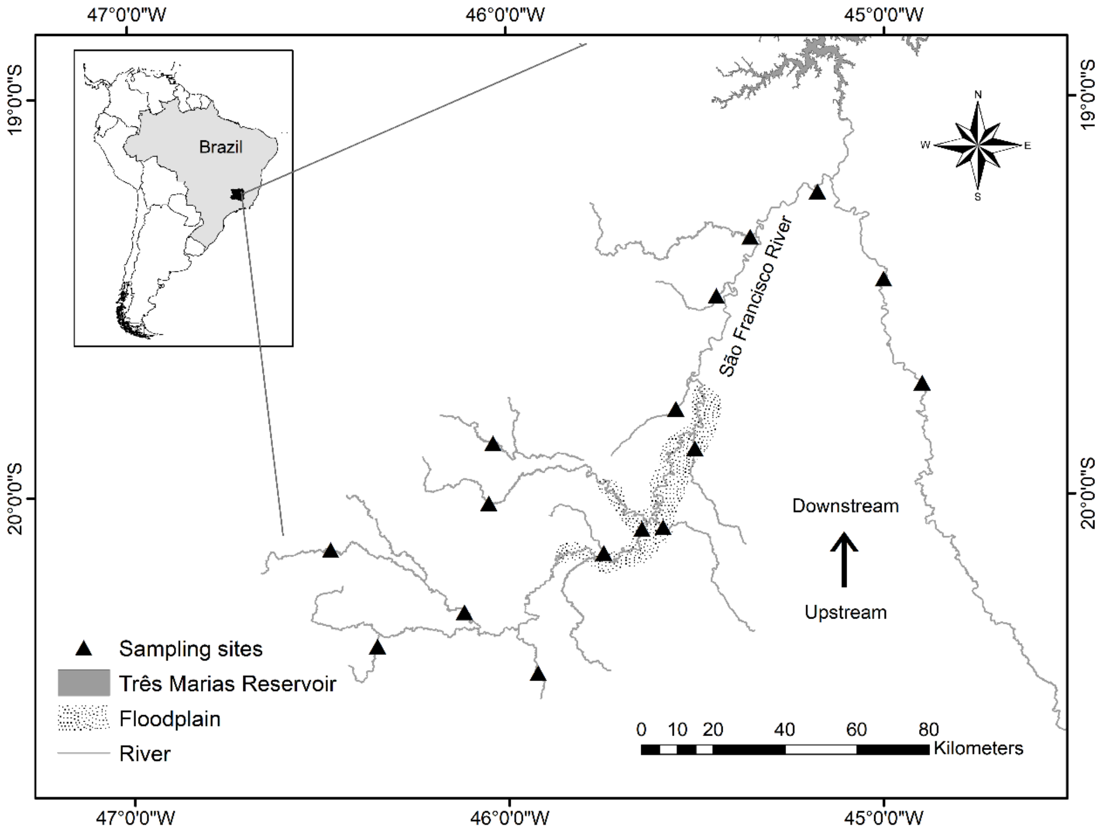

FIGURE 1. Map of the Upper São Francisco River Basin, indicating the sampling sites and the location of the floodplain.

Sampling

We selected 16 rivers, with average flows ranging from 0.70 m^3/s to 136 m^3/s, distributed along the entire basin (Figure 1). Each river was sampled once in September or November 2020. Fishes were captured using a cast net (1.5 cm mesh between opposite nodes) with an effort of two hours per river. As soon as the fish were caught, we identified, measured, and weighed them before their release. The individuals who could not be identified in the field were euthanized in a eugenol solution, fixed in 10% formaldehyde, and brought to the laboratory, where they were transferred to 70% alcohol.

The mean long-term flow was used as a proxy of river size. These data were obtained for each river through the shapefile of the São Francisco River Basin, created by the Instituto Mineiro de Gestão das Águas and in the report of the Serviço Geológico do Brasil (Pinto & Alves, 2001). We also calculated the fluvial distance to Três Marias reservoir for each sampling site using Google Earth Pro 7.3.3.7786 software. This variable was used to assess the position of the rivers in the basin.

Data analyses

We classified each individual of the migratory species as juvenile or adult based on the available literature on their size at first maturity (Andrade et al., 2004; Boncompagni-Júnior et al., 2013; da Graça & Pavanelli, 2007; Godinho & Godinho, 2003a; Rizzo et al., 1996; Thomé et al., 2005).

To understand the role of the size of the rivers in the life cycle of migratory fish, we built generalized linear models (GLMs). The dependent variables that we evaluated were fish abundance and richness, considering all the sampled species, migratory species, and juveniles of the migratory species. We also investigated the mean length of *Prochilodus costatus* Valenciennes 1850 and *Salminus hilarii* Valenciennes 1850, which were the most captured migratory species. We tested whether the variables mentioned above were driven by the fluvial distance from the Três Marias reservoir and the long-term river average flow. The latter was log-transformed for better graphical visualization.

We considered the proper distribution for each GLM the one that had the least overdispersion and that was suitable for the nature of the dependent variable (Zuur et al., 2009). All statistical analyses were performed using RStudio 1.3.959 (R Core Team, 2021). Multicollinearity and pseudo-R^2 were calculated for all GLMs. For the former we used car package (Fox & Weisberg, 2019) and for the GLMs, the stats package (R Core Team, 2021).

RESULTS

We collected 500 individuals from 29 species of fishes (Supplementary 1). Most of the individuals (52%) were juveniles belonging to three migratory species: *P. costatus*, *S. hilarii* and *Prochilodus argenteus* Spix & Agassiz 1829 (Figure 2).

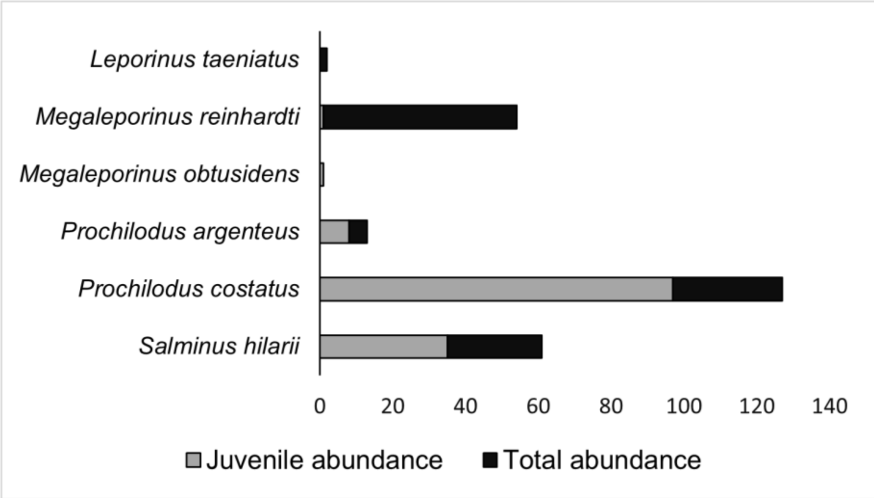

FIGURE 2. Total and juvenile abundance of the sampled migratory species.

None of the evaluated variables explained the total abundance of migratory fishes. However, the abundance of the juveniles was explained by the fluvial distance from the Três Marias reservoir (Figure 3; Table 1). The greatest abundances were found at intermediate distances, between 100 km and 250 km upstream from the reservoir.

TABLE 1. Variables and parameters for each significative (p<0.05) GLM.

Dependent variable	**Independente variables**	**Distribuition**	**p**	**Pseudo R^2**
Juvenile's migratory abundance	Três Marias reservoir fluvial distance	Negative binomial	0.00207	22.13
Juvenile's migratory species richness	Três Marias reservoir fluvial distance	Poisson	0.02169	29.42
Migratory species richness	River flow	Poisson	0.03962	20.68
Species richness	River flow	Negative binomial	0.000998	35.21
P. costatus mean size	River flow	Gaussian	0.01994	43.33

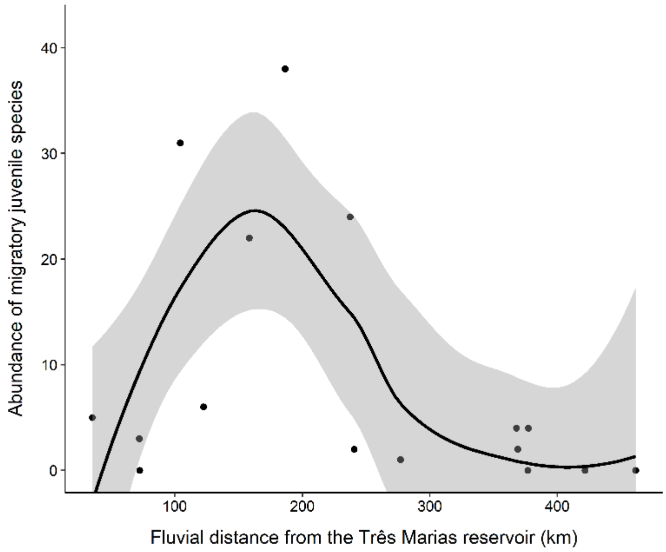

FIGURE 3. Relationship between the abundance of migratory juvenile species and fluvial distance from the Três Marias reservoir.

River flow was the main variable that explained species richness, for both the species in general (Figure 4; Table 1) and the migratory species (Figure 5). However, we did not observe this same relationship when considering only juvenile individuals of migratory species. In this case, richness was only negatively related to the river distance from the Três Marias reservoir (Figure 6; Table 1).

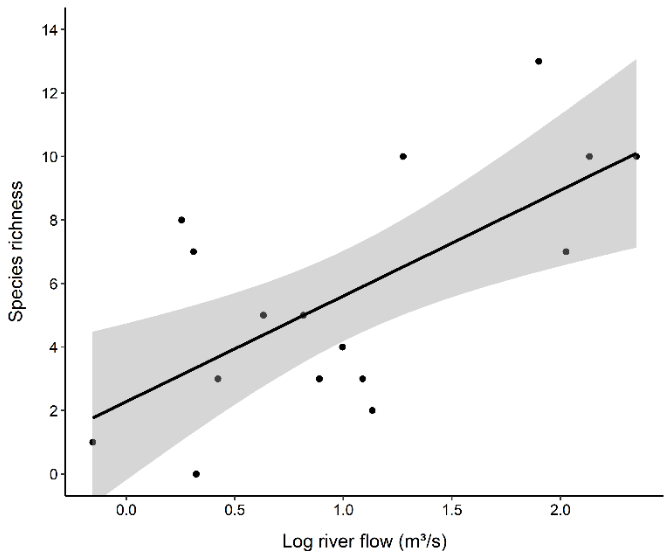

FIGURE 4. Relationship between species richness and river flow (log).

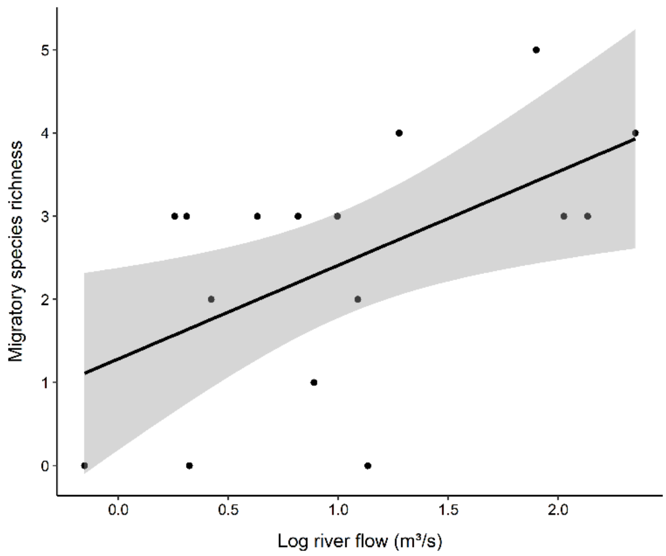

FIGURE 5. Relationship between migratory species richness and river flow (log). Regression line in black, and the confidence interval in grey.

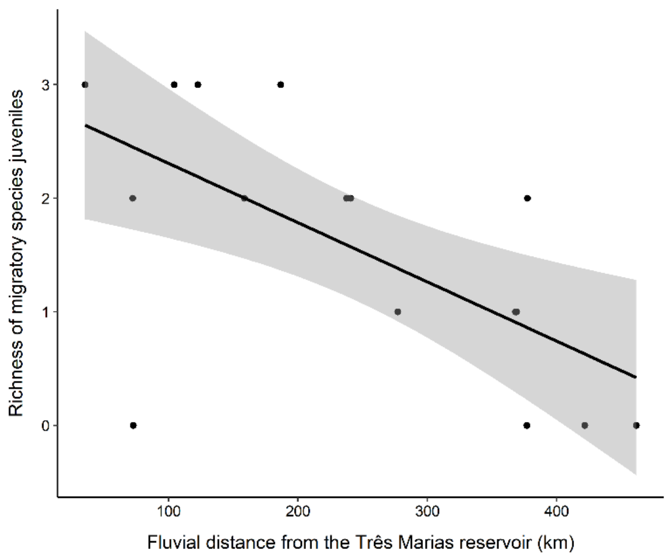

FIGURE 6. Relationship between the richness of migratory juvenile species and the fluvial distance from the Três Marias reservoir.

Although *P. costatus* and *S. hilarii*, the most abundant species in the catches, were tested, the relationship between the mean size of individuals and river flow was observed only for the former (Figure 7; Table 1).

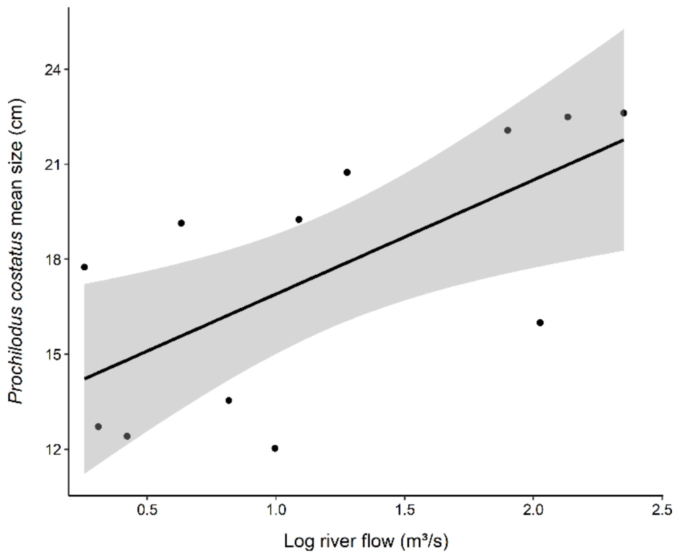

FIGURE 7. Relationship between the mean size of *Prochilodus costatus* and river flow (log).

DISCUSSION

We found that smaller rivers are important environments in migratory species life cycle. These environments, especially when draining regions close to floodplains, seem to be the first places where juveniles of migratory species move after leaving the floodplain lagoons. We have also provided information indicating that individuals move along rivers as they grow, being found in increasingly larger rivers.

The greatest abundance of juveniles was found in the middle portion of the upper São Francisco Basin (intermediate distances from the Três Marias reservoir), which presents an extensive floodplain area, with approximately 81 marginal lagoons (Sato, Cardoso, & Amorim, 1988). Five of our sample points are located in this region, and three of them had an abundance of juveniles three to six times greater than those in other areas. Thus, it is likely that juveniles will look for close rivers immediately after leaving floodplain lagoons.

The total species richness and migratory species richness showed a positive relationship with river size, while the juvenile richness increased towards the lowest portion of the basin. This pattern was expected, as the increase in fish richness with increasing river order, that is, downstream, has already been described in the literature (Platts, 1979; Jackson, Peres-Neto, & Olden, 2001; Cheng et al., 2016). Smaller rivers do not support high diversities and more structured fish assemblages (Jackson, Peres-Neto, & Olden, 2001). While larger rivers, in addition to more space, have greater habitat heterogeneity, which allows the presence of species with different habits, both feeding and behavioural. Furthermore, in comparison to smaller rivers, larger rivers are not as affected by local precipitation (Welcomme, 1985; Junk, Bayley, & Sparks, 1989), so their physicochemical conditions do not fluctuate unpredictably, making these environments more stable (Harrel & Dorris, 1968).

Although the relationship between abundance and river size was not observed, when considering only migratory juveniles, our results indicated that the size of individuals of *P. costatus* increases with the size of the river. These data suggest that juveniles of this species show a gradual displacement towards larger rivers throughout their growth. Therefore, with the increase in the size of the river, an increase in the biomass of migratory species would be expected without the need for an increase in their number. This displacement probably occurs to avoid predation in the first stages of life, as previously proposed (Godinho & Pompeu, 2003), while looking for more suitable areas to optimize growth by avoiding competition, finding more productive environments and reducing energy expenditure (Lucas et al., 2001b). On the other hand, *S. hilarii*, the only other migratory species for which the existence of this pattern could be assessed, did not show this relationship. Populations of this species mainly inhabit smaller tributaries, and individuals, even adults, are rarely found in main channels (Agostinho et al., 2004).

Studies documenting the movement of juvenile migratory species report that important migration occurs upstream to join the adults of their populations, a process known as “arribação” in the São Francisco Basin (Godinho & Kynard, 2006; Prado et al., 2016; Silva & Stewart, 2017). Although our work did not investigate “arribação”, the results with *P. costatus* demonstrate that juveniles have more complex movement patterns than just longitudinal migration, as they use rivers of different sizes throughout their development. Thus, we suggest that at least for *P. costatus*, juveniles return to rivers and move towards smaller and close rivers after their initial development in the lentic regions of floodplains. As individuals develop, they move downstream in search of their definitive feeding site. Once at this location, they remain during the dry season, accumulate energy, and develop their gonads to prepare for the migratory event that occurs during the rainy season (Figure 8).

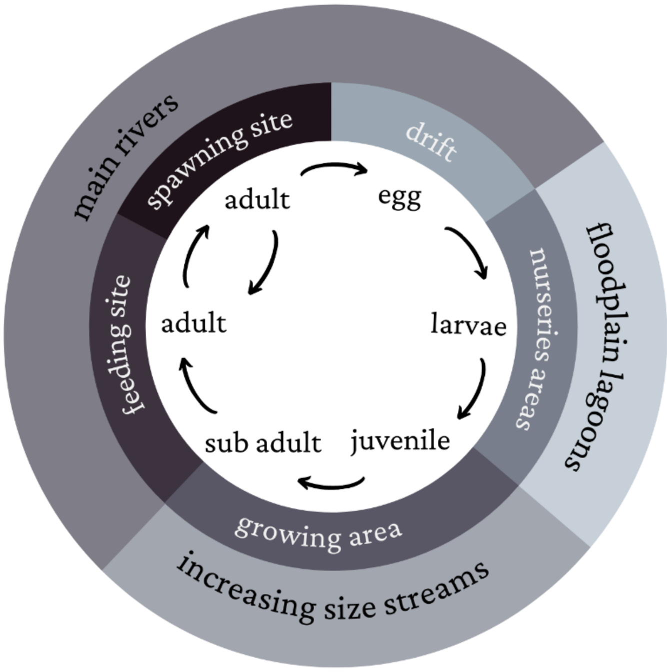

FIGURE 8. Proposed life cycle model of the migratory fishes of the upper São Francisco River Basin (based on *Prochilodus costatus* data).

Brazilian law considers that small hydropower plants (< 10 GW) (Brasil, 1986) present nonsignificant impacts and do not need more extensive studies of environmental impacts (Brasil, 2001). These small hydropower plants are usually built in small rivers, and here, we show that these rivers can also be fundamental for large migratory fishes, although these fish are usually associated with larger rivers. The abovementioned law provides a simplified environmental assessment of the impacts prior to construction, but our results suggest that even the impacts of small hydroelectric powerplants built on small rivers can be significant and must be investigated prior to construction.

Studies focused on the movement of juveniles are still needed, seeking to understand, for example, which factors lead to their progressive displacement and whether the individuals arrive at the feeding site already as adults or during their development. We hope that our results will contribute to a better understanding of the life cycle of freshwater migratory species since different anthropic activities threaten their habitats, and some of these species are already facing extinction. Currently, the best known strategy for the conservation of neotropical migratory fishes is the maintenance of free-flowing stretches encompassing all necessary habitats for completing their life cycle, usually including feeding and reproductive sites. Here, we conclude that it is also necessary to include small tributaries of main channels and floodplain regions in these protected free-flowing stretches.

ACKNOWLEDGMENTS

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DATA AVAILABILITY STATEMENT

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDICE

SUPPLEMENTARY 1. Species and number of individuals captured.

Taxon	**Abundance**
Characiformes	
Acestrorhynchidae	
Acestrorhynchinae	
Acestrorhynchus lacustris (Lütken 1875)	6
Anostomidae	
Leporellus vittatus (Valenciennes 1850)	1
Leporinus piau Fowler 1941	8
Leporinus taeniatus Lütken 1875	2
Megaleporinus obtusidens (Valenciennes 1837)	1
Megaleporinus reinhardti (Lütken 1875)	54
Bryconidae	
Salmininae	
Salminus hilarii Valenciennes 1850	61
Characidae	
Stethaprioninae	
Astyanax lacustris (Lütken 1875)	3
Psalidodon fasciatus (Cuvier 1819)	26
Curimatidae	
Curimatella lepidura (Eigenmann & Eigenmann 1889)	8
Cyphocharax gilbert (Quoy & Gaimard 1824)	2
Steindachnerina elegans (Steindachner 1875)	6
Erythrinidae	
Hoplias intermedius (Günther 1864)	3
Prochilodontidae	
Prochilodus argenteus Spix & Agassiz 1829	13
Prochilodus costatus Valenciennes 1850	127
Serrasalmidae	
Serrasalminae	
Metynnis maculatus (Kner 1858)	2
Myleus micans (Lütken 1875)	2
Serrasalmus brandtii Lütken 1875	14
Triportheidae	
Triportheinae	
Triportheus guentheri (Garman 1890)	27
Perciformes	
Sciaenidae	
Pachyurus francisci (Cuvier 1830)	1
Pachyurus squamipennis Agassiz 1831	2
Siluriformes	
Heptapteridae	
Rhamdiinae	
Rhamdia quelen (Quoy & Gaimard 1824)	2
Loricariidae	
Loricariinae	

Harttia sp.	2
Hypostominae	
Hypostomus spp.	5
Hypostomus affinis (Steindachner 1877)	5
Hypostomus francisci (Lütken 1874)	1
Hypostomus margaritifer (Regan 1908)	4
Pimelodidae	
Pimelodus fur (Lütken 1874)	76
Pimelodus maculatus Lacepède 1803	9

ARTIGO 2

DOES RIVER ORDER DRIVE NEOTROPICAL FISH DIVERSITY PATTERNS?

Artigo redigido conforme as normas da revista Biota Neotropica.

Does river order drive neotropical fish diversity patterns?

Marina F. Moreira[1]; Miriam A. Castro[2]; Paulo S. Pompeu[1]

[1]Laboratório de Ecologia de Peixes, Programa de Pós-Graduação em Ecologia Aplicada, Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras – UFLA, Campus Universitário, 37200-900, Lavras, Minas Gerais, Brasil.
[2] Cemig Geração e Transmissão, Gerência de Gestão Ambiental, Av. Barbacena, 1200, 12º andar, Ala A2, 30190-131, Belo Horizonte, MG, Brasil.

Abstract

One of the aspects of the habitats in freshwater environments that can influence the structure and dynamics of fish communities is the size of the river, which is often represented by its order and reflects the connectivity between rivers. However, few studies have investigated this relationship, and recent publications are absent. Therefore, our work aimed to understand the relationship between the size of a river, in this case, its order, and the diversity patterns of the fish community, evaluating alpha and beta diversities. We analyzed the fish communities of 48 rivers from the first to the fifth order along the upper São Francisco River Basin. Our study added 34 additional species from lotic stretches that had not been registered yet for this region. We found high values for alpha and beta diversities with turnover being the main process leading to the species variation among the rivers of all orders. The alpha diversity showed an increase with the size of the river while the beta diversity does not seem to have a clear pattern related to the river size. We highlighted the important and little explored, role of intermediate-sized rivers in maintaining biodiversity and indicated that several additional species can still be recorded within this region.

Key words: alpha diversity; beta diversity; species turnover; river size; fish communities.

A ordem dos rios direciona os padrões de diversidade de peixes neotropicais?

Resumo

Um dos aspectos dos habitats em ambientes de água doce que pode influenciar na estrutura e dinâmica das comunidades de peixes é o tamanho do rio. Este muitas vezes é representado por sua ordem e reflete a conectividade entre os rios. No entanto, poucos estudos investigaram essa relação e existe uma ausência de publicações recentes. Portanto, nosso trabalho teve como objetivo entender a relação entre tamanho do rio, neste caso, sua ordem, e os padrões de diversidade da comunidade de peixes, avaliando as diversidades alfa e beta. Analisamos as comunidades de peixes de 48 rios de primeira a quinta ordem ao longo da Bacia do Alto São Francisco. Nosso estudo adicionou 34 espécies de trechos lóticos que ainda não haviam sido registrados para esta região. Encontramos altos valores para as diversidades alfa e beta, sendo o turnover o principal processo que leva a variação de espécies entre os rios de todas as ordens. A diversidade alfa aumentou com o tamanho do rio, enquanto a diversidade beta não parece ter um padrão claro relacionado a este. Destacamos o importante e pouco explorado papel dos rios de médio porte na manutenção da biodiversidade e indicamos que várias espécies adicionais ainda podem ser registradas nesta região.

Palavras-chave: diversidade alfa; diversidade beta; turnover; tamanho do rio; comunidades de peixes.

Introduction

Biological communities are structured through the interaction between abiotic and biotic factors, such as the aspects of the species' habitat and the interactions between organisms. The relationship between the structure of the ichthyofauna in freshwater ecosystems and its physical structure is widely studied, with a focus on characteristics of its physical habitat, and on the effects of land use changes in the watershed (Pusey, Arthington, & Read, 1993; Jackson, Peres-Neto, & Olden, 2001; Felipe & Súarez, 2010; Kumar, Uttam, & Sarkar, 2012; Leal et al., 2014; D. R. De Carvalho et al., 2015; C. C. Arantes et al., 2017). One of the aspects of the habitat that can influence the structure of its communities is the size of the river, which is often represented by its order. However, few studies have investigated this relationship (Platts, 1979; Barila, Williams, & Stauffer, 1981; Paller, 1994; Radinger & Wolter, 2014) and recent publications are absent.

The connectivity of rivers with other tributaries is also responsible for the dynamics and structuring of fish communities (Shao et al., 2019). Connectivity is closely related to the river order which, by reflecting its hierarchical position in the drainage, also reflects how potentially isolated it is from the central regions of the basin (Strahler, 1957). Thus, rivers of lower orders, the headwaters, have greater isolation from the central portions of the basin, while those of higher orders and, consequently, those downstream have greater connectivity with other tributaries (Leibowitz et al., 2018). Through the connectivity of rivers, fish are able to disperse and have access to different resources such as food, refuge from predators, and spawning grounds, in addition to avoid unfavorable conditions (Bowler & Benton, 2005). Moreover, connectivity allows individuals to colonize new locations, contributing to the maintenance of populations in the long term (Jackson, Peres-Neto, & Olden, 2001; Shao et al., 2019).

The study of community diversity patterns can be the key to assessing how habitat characteristics influence their dynamics, as it can provide an understanding of which physical characteristics allow or inhibit the establishment of certain species. By studying the alpha, beta, and gamma diversities of a region, we can assess how the dynamics of communities occur along a spatial gradient (Socolar et al., 2016; Zbinden & Matthews, 2017). Alpha diversity refers to the average species richness of a location, while beta shows the variation in species composition between locations in a region, and gamma presents the total richness of the region (Whittaker, 1972).

Understanding beta diversity is especially important as it makes it possible to infer which mechanisms generate diversity patterns in the community of a region (Baselga, 2010; Socolar et al., 2016; Peláez, Azevedo, & Pavanelli, 2017). These patterns can occur through two processes: nestedness and turnover. The former occurs when there is a loss of species along a gradient, so that communities at each location represent a portion of the total richness of a region (Wright & Reeves 1992), while species replacement among local assemblages occurs in the turnover process (Baselga, 2010).

Our work aimed to understand the relationship between the size of a river, in this case, its order, and the diversity patterns of the fish community, evaluating alpha and beta diversities. We hypothesized that rivers of higher orders have higher alpha diversities, while higher beta diversities are found in rivers of lower orders due to their isolation from central areas of the basin.

Material and Methods

1. Study area

The São Francisco River Basin is the largest one located entirely within the Brazilian territory. It is divided into four regions: upper, middle, sub-middle, and lower São Francisco. At least 240 native fish species are known from the entire basin, 60% of which are endemic (Barbosa et al. 2017). Our study was carried out in the upper São Francisco region, upstream from the Três Marias Reservoir, the first big reservoir along the São Francisco mainstream. Fish inventories in the upper region are rare and have investigated the fish fauna of the headwaters (Casatti & Castro, 1998; Casarim, Caldeira, & Pompeu, 2020) and the floodplains (Sato, Cardoso, & Amorim, 1988).

2. Sampling

We randomly selected first to fifth-order rivers (sensu Strahler) along the upper São Francisco Basin, totaling 48 rivers, distributed as follows: 1st order = 7, 2nd order = 8, 3rd order = 16, 4th order = 12, and 5th order = 5. Each river was sampled once. The sampling was carried out in three campaigns, in September 2010, September 2020, and November 2020.

We collected the fish in each river with a sampling effort of two people for two hours. We used semicircular sieves (80 cm in diameter and 1.0 mm mesh) and a trawl net (3 m long and 1.5 m high with mesh of 5.0 mm internodes), the latter being performed only when there was a suitable environment. After being captured, they were euthanized in eugenol solution, fixed in 10% formaldehyde, and taken to the laboratory where they were washed, transferred to 70% alcohol, and taxonomically identified.

The river order data, referring to each sampled point, were obtained through the shapefile of the São Francisco Basin, available on the website of Sistema Estadual de Meio Ambiente e Recursos Hídricos (https://idesisema.meioambiente.mg.gov.br/).

3. Data analyses

The Venn Diagram was performed on the website of The Bioinformatics and Evolutionary Genomics group (http://bioinformatics.psb.ugent.be/webtools/Venn/).

All the others analyses were made in RStudio version 1.4.1106 (R Core Team, 2021). We calculated the beta diversity partition using the betapart package (Baselga et al. 2021). The analysis of alpha diversity as well as species accumulation curves were performed with the vegan package (Oksanen et al. 2020).

Results

We sampled a total of 64 species distributed in six different orders, most of them Characiformes (31 species) and Siluriformes (27 species). Together, these two orders contributed to 92% of the species recorded in the present study. Two recorded species (*Knodus moenkhausii* and *Poecilia reticulata*) are nonnative (Barbosa et al., 2017; Bueno et al., 2021), and *Brycon nattereri* is classified as vulnerable in Brazil and endangered in the state of Minas Gerais (ICMBio/MMA, 2018) (Table 1).

Table 1. Fish species sampled from each river order (sensu Strahler) on the upper São Francisco River Basin in the state of Minas Gerais, Brazil. [1] nonnative species; [2] endangered species.

	River order				
Taxon	**1**	**2**	**3**	**4**	**5**
Characiformes					
Anostomidae					
Leporinus marcgravii Lütken 1875			x	x	
Leporinus taeniatus Lütken 1875			x		
Megaleporinus reinhardti (Lütken 1875)					x
Bryconidae					
Bryconinae					
Brycon nattereri [2] Günther 1864	x				
Salmininae					
Salminus hilarii Valenciennes 1850			x		
Characidae					
Cheirodontinae					
Serrapinnus heterodon (Eigenmann 1915)		x	x	x	x
Serrapinnus piaba (Lütken 1875)			x	x	x
Stethaprioninae					
Astyanax lacustris (Lütken 1875)	x	x	x	x	
Deuterodon intermedius (Eigenmann 1908)	x	x	x		
Hasemania nana (Lütken 1875)			x	x	
Hemigrammus marginatus Ellis 1911			x	x	
Hyphessobrycon santae (Eigenmann 1907)	x	x	x	x	
Moenkhausia sanctaefilomenae (Steindachner 1907)			x	x	
Oligosarcus argenteus Günther 1864			x		
Psalidodon bockmanni (Vari & Castro 2007)	x	x	x	x	x
Psalidodon fasciatus (Cuvier 1819)	x	x	x	x	x

Psalidodon rivularis (Lütken 1875)	x	x	x	x	x
Stevardiinae					
Hysteronotus megalostomus Eigenmann 1911			x		
Knodus moenkhausii [1] (Eigenmann & Kennedy 1903)	x	x	x	x	
Lepidocharax burnsi Ferreira, Menezes & Quagio-Grassiotto 2011				x	
Piabarchus stramineus (Eigenmann 1908)			x		
Piabina argentea Reinhardt 1867		x	x	x	x
Planaltina sp.		x	x	x	
Crenuchidae					
Characidiinae					
Characidium fasciatum Reinhardt 1867	x	x		x	x
Characidium lagosantense Travassos 1947		x	x	x	x
Characidium zebra Eigenmann 1909	x	x	x	x	x
Erythrinidae					
Hoplias intermedius (Günther 1864)		x	x	x	
Hoplias malabaricus (Bloch 1794)				x	
Parodontidae					
Apareiodon ibitiensis Amaral Campos 1944			x		
Apareiodon piracicabae (Eigenmann 1907)	x		x		
Parodon hilarii Reinhardt 1867		x		x	x
Cyprinodontiformes					
Poeciliidae					
Poeciliinae					
Phalloceros uai Lucinda 2008				x	x
Poecilia reticulata [1] Peters 1859			x	x	
Gymnotiformes					
Gymnotidae					
Gymnotinae					
Gymnotus carapo Linnaeus 1758	x		x	x	
Sternopygidae					
Eigenmanniinae					
Eigenmannia besouro Peixoto & Wosiacki 2016		x	x		x
Perciformes					
Cichlidae					
Cichlinae					
Geophagus brasiliensis (Quoy & Gaimard 1824)				x	
Siluriformes					
Aspredinidae					
Aspredininae					
Bunocephalus hartti Carvalho, Cardoso, Friel & Reis 2015					x
Bunocephalus minerim Carvalho, Cardoso, Friel & Reis 2015					x
Auchenipteridae					
Auchenipterinae					
Trachelyopterus galeatus (Linnaeus 1766)			x		
Heptapteridae					
Heptapterinae					
Cetopsorhamdia iheringi Schubart & Gomes 1959		x	x	x	x
Imparfinis minutus (Lütken 1874)		x	x	x	x

Phenacorhamdia tenebrosa (Schubart 1964)		x	x	x	
Rhamdiopsis microcephala (Lütken 1874)			x	x	
Rhamdiinae					
Pimelodella lateristriga (Lichtenstein 1823)	x		x		
Pimelodella laurenti Fowler 1941			x	x	
Pimelodella vittata (Lütken 1874)					x
Rhamdia quelen (Quoy & Gaimard 1824)			x		x
Loricariidae					
Hypoptopomatinae					
Hisonotus alberti Roxo, Silva, Waltz & Melo 2016	x		x	x	x
Hisonotus vespuccii Roxo, Silva & Oliveira 2015					x
Neoplecostomus sp.			x		
Hypostominae					
Hypostomus sp.			x	x	x
Hypostomus sp. 2	x	x	x	x	
Hyposyomus sp. 3		x			x
Loricariinae					
Harttia longipinna Langeani, Oyakawa & Montoya-Burgos 2001					x
Harttia sp.			x	x	x
Rineloricaria sp.				x	x
Pseudopimelodidae					
Batrochoglaninae					
Microglanis leptostriatus Mori & Shibatta 2006	x		x	x	
Pseudopimelodinae					
Pseudopimelodus charus (Valenciennes 1840)			x		x
Trichomycteridae					
Stegophilinae					
Stegophilus insidiosus Reinhardt 1859					x
Trichomycterinae					
Cambeva concolor (Costa 1992)				x	
Cambeva variegata (Costa 1992)	x	x	x	x	x
Trichomycterus brasiliensis Lütken 1874	x	x		x	
Trichomycterus reinhardti (Eigenmann 1917)	x	x	x		
Synbranchiformes					
Synbranchidae					
Synbranchus marmoratus Bloch 1795	x	x			x

[1] non native
[2] endangered

Only five species were shared by all river orders: *Cambeva variegata, Characidium zebra*, *Psalidodon bockmann*, *P. fasciatus e P. rivularis* (Figure 1, Table 1). In addition, rivers of orders greater than three presented more exclusive species than the smaller ones. The species accumulation curves did not show stabilization for any of the rivers' orders, not even the ones with the highest number of sample sites, but for fifth order rivers, many species were recorded even with few rivers sampled (Figure 2).

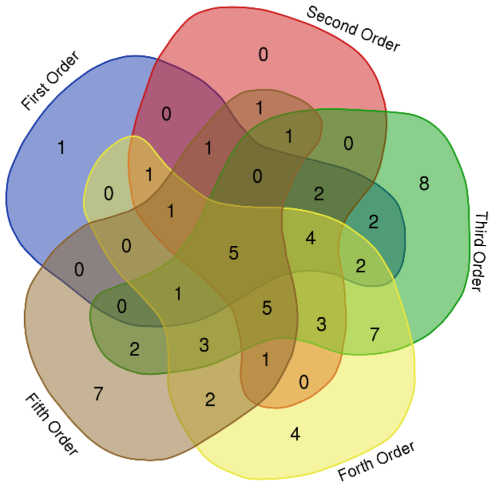

Figure 1. Venn Diagram with the number of exclusive and shared species between river orders from the upper São Francisco River Basin.

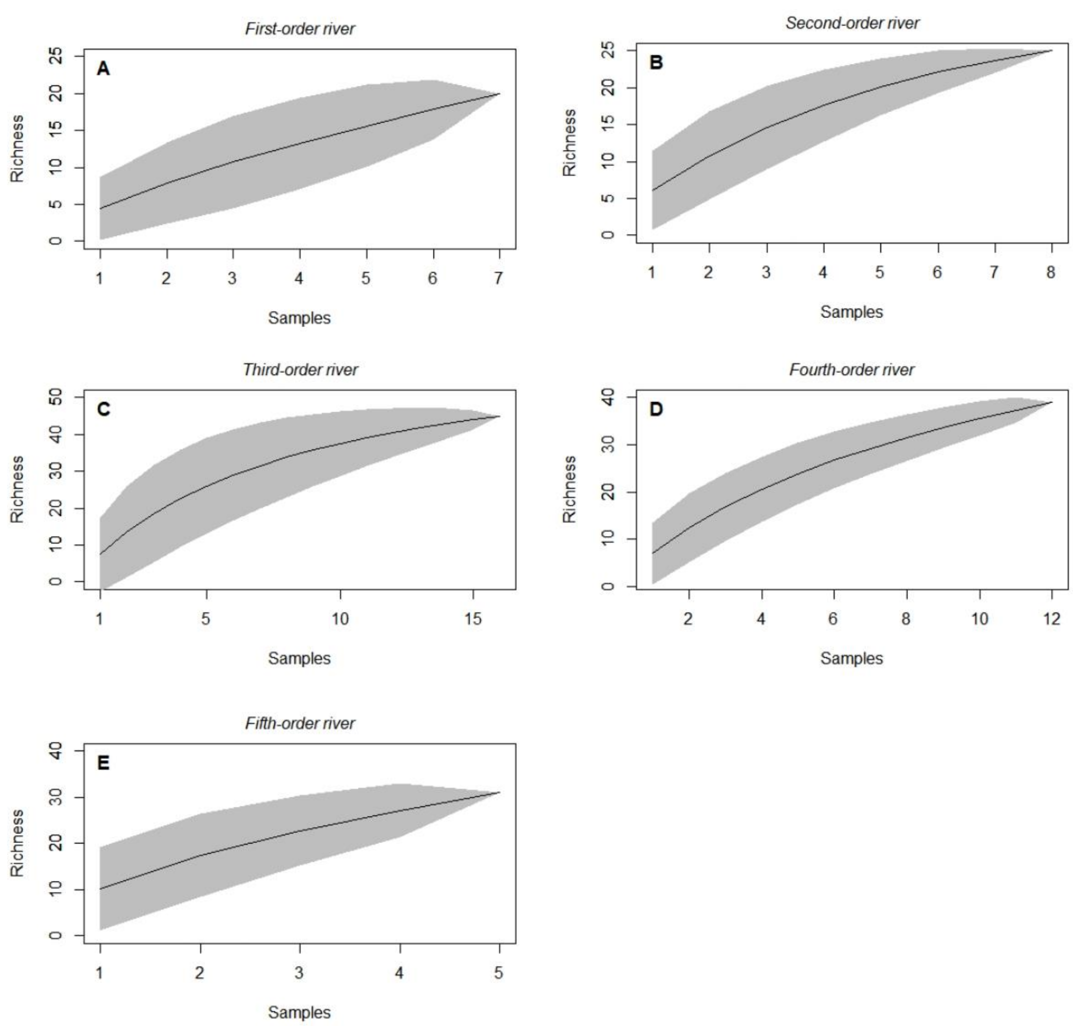

Figure 2. Fish species accumulation curves from first (A), second (B), third (C), fourth (D) and sixth (E) order river.

The mean alpha for each river order ranged between four to ten species, and in general, we observed an increase in richness following the river order (Figure 3). However, third-order streams were the ones with a larger variation of such parameter (2 to 20 species).

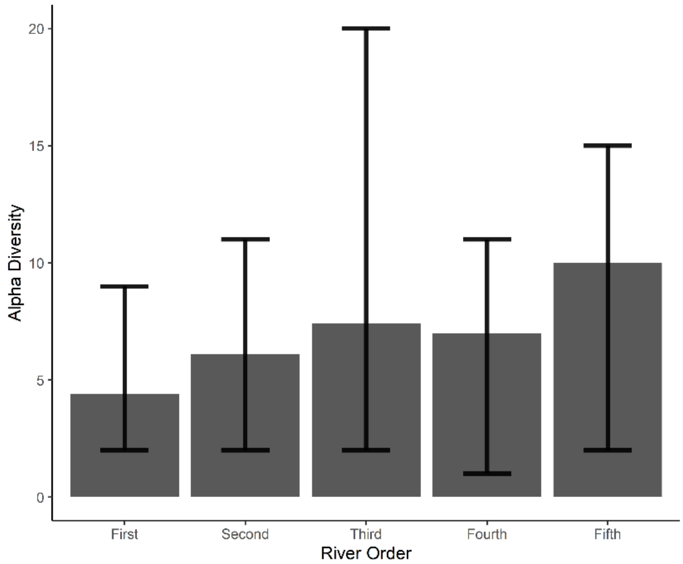

Figure 3. Alpha diversity for each river order with mean alpha (gray bar) and maximum and minimum alpha (range bar).

All river orders showed high values of beta diversity (around 70%), but these values do not seem to be related to river order. The turnover was the main process leading to the species variation among the rivers of all orders (Figure 4), with values ranging from 67% to 83%.

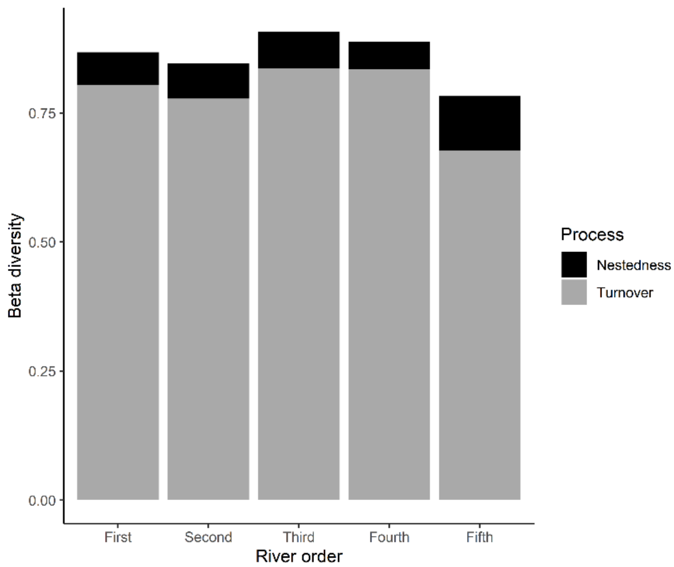

Figure 4. Beta diversity partition for each river order.

Discussion

We found high values for alpha and beta diversities. Although the alpha diversity indeed showed an increase with the size of the river, the beta does not seem to have a clear pattern related to the river size, contrary to what we expected.

Fish inventories from the region upstream Três Marias Reservoir were available only for the headwaters and floodplain areas (Sato, Cardoso, & Amorim, 1988; Casatti & Castro, 1998; Casarim, Caldeira, & Pompeu, 2020). Even focusing on the small fauna, our study added 34 additional species from lotic stretches that had not been registered yet. Nevertheless, even more species are expected to be found in this region since for none of the orders there was a stabilization of the accumulation curves. This result indicates that a greater sampling effort than what we performed is required to fully sample the community of different sizes of rivers for this region since an increase in sampling effort leads to an increase in the number of species collected (Pompeu et al., 2021).

The Venn Diagram showed not only the importance of higher-order rivers in harboring species that only exist in these environments, but also that there is a continuous replacement of species with the increase in river size since only five species were common in all river sizes. All five species are small fishes, three of them are tetra fish (*Psalidodon* spp.), while two are fishes associated with the substrate (*C. variegata* and *C. zebra*) (Britski, Sato, & Rosa, 1988; Vieira, Santos, & Alves, 2005). Although the larger rivers presented a greater number of exclusive species, this was not a continuous increase since the third-order rivers presented a greater number of species. This fact is possibly related to our sampling effort since the largest number of rivers collected was of this size.

The observed alpha diversity is similar to those reported to different Brazilian biomes (Leal et al., 2014; Silva-Oliveira, Canto, & Ribeiro, 2016; Claro-García, Assega, & Shibatta, 2018), however, these values are rarely evaluated by river order. Here we notice higher alpha diversity in the bigger rivers, with a gradual increase in these values as the river size increases. Similar results were also found by other authors (Whiteside & McNatt, 1972; Platts, 1979; Bistoni & Hued, 2002), but most of the studies are in basins of the temperate region, and recent publications that evaluate these relationships are absent. These two patterns are possibly related to the greater area existing in bigger rivers (Macedo et al., 2014; Oberdorff et al., 2019) in addition to the greater connectivity to other tributaries of the basin (Shao et al., 2019) and greater stability of conditions (Harrel & Dorris, 1968; Whiteside & McNatt, 1972).

The third-order rivers were the ones that showed the greatest variation in alpha diversity, and this may be related to three factors: (1) the greatest sampling effort occurred in these environments, (2) there is great variation in their size, due to their hierarchical structure, and (3) the possibility that some of these rivers are being repopulated by fish from larger rivers (Whiteside & McNatt, 1972).

High values of beta diversity related to the turnover process have also been reported for other Neotropical basins (Pompeu et al., 2019). In our study, we prove that such a pattern is valid for different river sizes. Thus, the difference in fish communities between rivers of different sizes occurs through the replacement of species, demonstrating that for this region, the fish communities of smaller rivers are not simply subsets of the communities of larger rivers (Baselga, 2010). Although we did not observe the decrease of beta diversity with the increase of river order as we hypothesized, it is possible that the different number of sampled rivers of each order has hidden a pattern. Nevertheless, it is important to highlight that even the largest rivers and, consequently, the ones less isolated showed high values of beta diversity. The beta diversity patterns that we found here demonstrate that fish assemblages from rivers of all sizes are the most important factors maintaining the regional richness (gamma diversity), rather than the sites with the greatest diversity. For the temperate region, conclusions similar to these have also been found (Zbinden & Matthews, 2017).

Our study was able to determine patterns of diversity in rivers of different orders in the upper São Francisco Basin and indicate that several additional species can still be recorded. Lastly, our study highlighted the important and little explored role of intermediate-sized rivers (3^{rd} – 5^{th} order) in maintaining biodiversity, as most studies focus only on headwaters (1^{st} – 2^{nd} order) or large rivers (above 6^{th} order).

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Author Contributions

Marina Ferreira Moreira: Contributed to the concept and design of the study, data collection, analysis and interpretation, and manuscript preparation.

Míriam Aparecida de Castro: Contributed to the data collection and critical revision.

Paulo dos Santos Pompeu: Substantial contribution in the concept and design of the study; data analysis and interpretation, manuscript preparation and critical revision.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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