UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
Câmpus de São José do Rio Preto

Francisco de Paula Severo da Costa Neto

Habitat use, trophic structure and functional diversity of fish in karst streams in the Brazilian Midwest

São José do Rio Preto
2021

Francisco de Paula Severo da Costa Neto

Habitat use, trophic structure and functional diversity of fish in karst streams in the Brazilian Midwest

Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biodiversidade, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Câmpus de São José do Rio Preto.

Orientadora: Profª. Drª. Lilian Casatti

São José do Rio Preto
2021

S498h

Severo-Neto, Francisco
Habitat use, trophic structure and functional diversity of fish in karst streams in the Brazilian Midwest / Francisco Severo-Neto. -- São José do Rio Preto, 2021
122 f. : il., tabs., fotos, mapas

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto
Orientadora: Lilian Casatti

1. Ecologia animal. 2. Ictiologia. 3. Comunidades ecológicas. 4. Riachos cársticos. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto. Dados fornecidos pelo autor(a).

Francisco de Paula Severo da Costa Neto

Habitat use, trophic structure and functional diversity of fish in karst streams in the Brazilian Midwest

Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biodiversidade, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Câmpus de São José do Rio Preto.

Comissão Examinadora

Profª. Drª. Lilian Casatti
UNESP – Câmpus de São José do Rio Preto
Orientador

Profª. Drª. Mônica Ceneviva Bastos
Universidade Estadual do Centro-Oeste – Unicentro

Prof. Dr. Camilo Andrés Roa-Fuentes
Universidad Pedagógica y Tecnológica de Colombia, UPTC

Prof. Dr. Maurício Cetra
Universidade Federal de São Carlos – São Carlos

Profª. Drª. Denise de Cerqueira Rossa Feres
UNESP – Câmpus de São José do Rio Preto

São José do Rio Preto
27 de outubro de 2021

A todos aqueles que acreditaram, inclusive eu.

AGRADECIMENTOS

Essa é uma Tese escrita basicamente por minhas duas mãos, mas que envolve tanta gente junto que eu espero fazer jus em palavras a tudo aquilo que me foi presentado por tantas pessoas maravilhosas, não só nesses quatro anos, mas por toda minha jornada.

Primeiramente, aos meus pais, João e Vera. Por sempre me darem suporte, amor, carinho, cuidado e tudo o mais que uma pessoa pode pedir. Todo esse caminho não seria possível se vocês não tivessem me estimulado e apoiado desde os primeiros aquários lá com 6 anos, quando começou toda essa paixão por peixes que me acompanha e fortalece até hoje. Aos meus irmãos, João Paulo e Ana Paula. Mesmo que a vida tenha separado a gente geograficamente por um tempo, vocês sempre estiveram e estarão no meu coração. Aos meus sobrinhos, Juína e Liduardo, por serem essas pessoinhas que me dão gás, me agitam, me expõem a essa alegria de ser tio, diariamente. A minha tia Nyda, por ter me recebido nos dias em que estive em Rio Preto, sempre com muito carinho e fazendo aquele strogonoff maravilhoso. Ao meu vô Sebastião, por ser realmente esse bastião de pessoa. Por toda essa sabedoria, exemplo, força e coragem que taí esbanjando dos seus 92 anos. Suas fotos de pescaria no projetor de slides antigo e todas as conversas pelo Pantanal, antes mesmo de eu saber onde ficava isso, foi a sementinha que hoje me fez ser completamente apaixonado por esse lugar e me sentir tão em casa nele. Como se ainda estivesse lá sentado no chão da sua sala comendo pipoca e ouvindo tudo com uma curiosidade gigantesca.

Aos meus colaboradores, Karol, Jaque e Fábio, que me ajudaram demaaais nesses finalmente, fosse com estatística, escrita ou motivação. Vocês são maravilhosos!

Às pessoas que foram fundamentais na minha vida, principalmente nesse último ano. Meu amigo Heriberto. Que honra poder te chamar de meu amigo, meu amigo. Você foi e é tão importante pra mim, em momentos que nem imagina. Obrigado por tudo. Por todos os campos, as conversas, por compartilhar todo seu amor pelos peixes, pela nossa trajetória

desde as reuniões na casa da sua mãe comendo bolo e tomando café. À Manu. Pela atenção, amizade, carinho, ensinamentos e por me fazer rir tantas vezes. Vocês dois são extremamente importantes e representam muito pra mim. Vocês acreditaram em mim quando eu mesmo duvidei. Difícil colocar em palavras quando a vontade era abraçar vocês e dizer tudo pessoalmente. Mas obrigado. De coração.

Ao Fábio Roque e Fundação Neotrópica, junto com Rodolfo, Anderson e Bruno, pelas coletas no rio Formoso através do Projeto Observágua.

À Tamires, pelos anos de companheirismo, paciência, compreensão e respeito. À Brigite, Frida, Amora, Miumiu e Afonso por serem esses seres maravilhosos que tanto amor me deram ao longo dos anos.

Aos meus amigos André, Cássio e Rafael. Nossa, vocês sempre surgiram na hora certa. Obrigado por todo o apoio, atenção, cuidado e risada que vcs me proporcionaram.

À ZUFMS, nas pessoas do Thomaz, Lili e Gustavo, por toda a ajuda, parceria e amizade. Por termos virado uma família.

Ao Ibilce e professor Kiko Langeani, por todo o apoio durante esses anos em que esteve diante da coordenação do programa;

Aos membros da banca, Profª. Drª. Mônica Ceneviva Bastos, Prof. Dr. Camilo Andrés Roa-Fuentes, Prof. Dr. Maurício Cetra e Profª. Drª. Denise de Cerqueira Rossa Feres, por dedicarem seu tempo e suas contribuições;

Ao Otávio. Pelas primeiras orientações. Por compartilhar comigo tanto conhecimento. Por ter me apresentado à Serra da Bodoquena. Pelos peixes. Pelas conversas sobre céu, a Terra, a água e o ar. Por ter me “ensinado” que os buracos nas rochas são feitos pelos *Ancistrus* girando bem rápido com os bigodes pra frente. Por ter sido meu confidente, meu pai postiço, meu amigo. Por ter esperado eu te visitar antes de partir. Por tudo. Fique bem. Saudades.

À Lilian, minha orientadora. Acho que você não tem ideia de qual honrado eu fico de te chamar de minha orientadora. Você é uma pesquisadora maravilhosa que eu já admirava (inclusive o primeiro artigo que eu li sobre peixes era seu), antes de ver a pessoa maravilhosa que você é. Obrigado pela oportunidade de ser seu aluno e de darmos esse passo juntos. Obrigado por toda atenção, compreensão, por me ajudar em diversos momentos e por acreditar em mim. Eu espero muito poder compartilhar outros trabalhos com você, já que distância e pandemia dificultaram um pouco a proximidade que eu gostaria. Mas foi lindo. Obrigado.

Ao Pantanal que tantas alegrias já me deu nesses 16 anos. Tanta história, aventura, perrengue, bicho, peixe, planta. E que agora queima enquanto eu escrevo essa Tese. Que hajam dias melhores pra você e que as pessoas tenham mais noção do quanto é importante.

Aos peixes que, desde pequeno, me ajudaram tanto a passar por crises e dificuldades, sem ter a menor consciência disso. Por estarem lá vivendo a vida deles tranquilamente enquanto tentamos encontrar padrões e encaixotá-los em espécies e categorias. Por ser o grupo de vertebrados mais legal do planeta (que me desculpem os outros, mas é verdade). Por tanta coisa que pude alcançar sendo uma ferramenta pra transmitir o que vocês não podem falar. Assim como o Pantanal, que sejam mais valorizados. Não no futuro, mas agora. Que seus ambientes sejam protegidos e não destruídos ou negligenciados para que as gerações futuras possam amá-los, assim como eu amo. Obrigado.

Nesse Mato Grosso desde os tempos de menino
Quando eu comecei a percorrer os seus caminhos
E desse chão eu fiz o meu lugar
Nos meus sonhos quis plantar
E a colheita há de vir (SATER, 1996)

RESUMO

Sistemas cársticos constituem ambientes único no mundo. Sua geomorfologia se baseia em rochas carbonáticas que agem como um filtro natural na hidrologia, resultando em ambientes aquáticos de alta transparência e beleza cênica extraordinária. Além de seu apelo visual, contribuem diretamente com o consumo de água por uma grande parcela da população mundial. Apesar destes fatores, ambientes cársticos são ameaçados pela ação humana, seja diretamente através da modificação do ambiente ou contaminação dos leitos por agentes defensivos e fertilizantes provindos do sistema agropecuário, ou indiretamente pelo aquecimento global. No Brasil, ambientes cársticos estão representados em sua maior parte na região Nordeste e Sudeste. Na região Centro-Oeste, próximo à fronteira com o Paraguai encontra-se o único sistema cárstico no estado de Mato Grosso do Sul, a Serra da Bodoquena, que consiste de um platô inserido na borda sul da bacia do Alto Paraguai, cujos tributários drenam para a planície do Pantanal Brasileiro. Trata-se de uma região mundialmente conhecida pelo turismo ecológico, especialmente para as atividades envolvendo seus rios cristalinos e a fauna de peixes residente. Embora a riqueza de espécies de peixes da região tenha seu consequente apelo no turismo e na manutenção da biodiversidade como um todo, informações básicas sobre sua biologia ainda são incipientes. Mais ainda, a região tem passado por mudanças quanto às atividades econômicas principais, com a substituição de pastagens por lavouras, porém, o consequente impacto dessas mudanças sobre peixes ainda é desconhecido. Sendo assim, o objetivo geral dessa Tese foi compreender como as espécies utilizam o ambiente (Capítulo 1), os recursos alimentares (Capítulo 2) e o efeito da paisagem na composição das comunidades (Capítulo 3). Para atingir esses objetivos, lançamos mão da classificação das espécies em grupos tróficos funcionais, que permitem a compreensão do uso da dimensão espacial pelos peixes dentro dos córregos e como e onde os recursos são obtidos por eles (Capítulo 1). Conhecendo o uso do espaço pelos peixes, determinamos quais itens fazem parte da dieta das espécies e como elas se relacionam na teia trófica regional (Capítulo 2). Encerramos investigando como a elevação e uso do solo atua sob a substituição de espécies e/ou atributos funcionais (Capítulo 3). Em suma, encontramos que: (1.) a maior parcela de peixes da região é de pequeno porte e contribui diretamente na riqueza de grupos funcionais tróficos; (2.) a dieta das espécies consiste basicamente de itens provenientes de fora do ambiente aquático e a rede trófica da comunidade apresenta alto grau de especialização, aninhamento e modularidade. Em outras palavras, um mesmo recurso pode ser partilhado entre várias espécies; entretanto, há aquelas que se especializam em determinado item, o que resulta na compartimentalização da comunidade com relação ao tipo de recurso consumido; (3.) A substituição de espécies/atributos funcionais não se relacionou com o uso do solo, mas sim com a altitude, mostrando que, no primeiro caso, fatores estocásticos estão envolvidos e no segundo, ambientais. Em conclusão, o conjunto de espécies de peixes da Serra da Bodoquena apresenta únicos padrões de uso de habitat, um reflexo da imposição ambiental da região, como uso de corredeiras; peixes pequenos usam principalmente margens e representam a maior parcela da riqueza da comunidade, evidenciando um padrão Neotropical; a partilha de recursos é alta e dependente de itens alóctones; e, no contexto da bacia do Alto Paraguai, o padrão singular de altitude da região é um fator fundamental na manutenção da diversidade de peixes.

Palavras–chave: Ictiologia. Comunidades. Água doce. Interações tróficas. Ecomorfologia. Diversidade Beta. Bacia do Alto Rio Paraguai. Serra da Bodoquena.

ABSTRACT

Karst systems constitute unique environments in the world. Its geomorphology is based on carbonate rocks that act as a natural filter in the hydrology, resulting in highly transparent aquatic environments and extraordinary scenic beauty. In addition to their visual appeal, they directly contribute to water consumption by a large portion of the world's population. Despite these factors, karst environments are threatened by human action, either directly through the modification of the environment or contamination of beds by defensive agents and fertilizers from the agricultural system, or indirectly by global warming. In Brazil, karst environments are mostly represented in the Northeast and Southeast regions. In the Center-West region, close to the border with Paraguay, the only karst system in the state of Mato Grosso do Sul is the Serra da Bodoquena which consists of a plateau inserted in the southern edge of the Upper Paraguay River basin, whose tributaries drain into the plain of the Brazilian Pantanal.

It is a region known worldwide for ecological tourism, especially for activities involving its crystalline rivers and resident fish fauna. Although the richness of fish species in the region has its consequent appeal for tourism and the maintenance of biodiversity as a whole, basic information about their biology still incipient. Furthermore, the region has undergone changes in terms of its main economic activities, with the replacement of pastures by crops, but the consequent impact of these changes on fish is still unknown. Therefore, the general objective of this Thesis was to understand how species use the environment (Chapter 1), the feeding resources (Chapter 2), and the effect of landscape on community composition (Chapter 3). To achieve these goals, we use the classification of species into functional trophic groups, which allow us to understand the use of the spatial dimension by fish within streams and how and where resources are obtained by them (Chapter 1). Knowing the use of space by fish, we determine which items are part of the species' diet and how they are related in the regional food web (Chapter 2). We close by investigating how elevation and land use act under the replacement of species and/or functional attributes (Chapter 3). In summary, we found that: (1.) the largest portion of fish in the region is small and contributes directly to the richness of trophic functional groups; (2.) the species' diet basically consists of items from outside the aquatic environment and the trophic network of the community presents a high degree of specialization, nestedness and modularity. In other words, the same resource can be shared among several species, although there are those that specialize in a certain item, which results in the compartmentalization of the community in relation to the type of resource consumed; (3.) The replacement of species/functional attributes was not related to land use, but rather to altitude, showing that, in the first case, stochastic factors are involved and, in the second, environmental ones. In conclusion, the set of fish species in Serra da Bodoquena presents unique patterns of habitat use, a reflection of the environmental imposition of the region; small fish mainly use margins and represent the largest portion of the richness of the community, evidencing a Neotropical pattern; resource sharing is high and dependent on allochthonous items; and, in the context of the Upper Paraguay basin, the region's unique altitude pattern is a fundamental factor in maintaining fish diversity.

Keywords: Ichthyology. Communities. Freshwater. Interações tróficas. Ecomorfology. Beta diversity. Upper Paraguay River basin. Serra da Bodoquena.

Summary

1 General Introduction

Karst systems are unique environments worldwide. Originally, its definition is based on bedrocks of carbonate limestones which are dissolved by the action of atmospheric carbon dioxide present on rainfall (Hartmann et al., 2014). Karst regions occupy 7-12% of the Earth's continental area and their aquifers represent a source of water to almost a quarter of the world's population (Ford & Williams, 2007). Despite their meaningfulness, the integrity of theses systems is threatened by the human action, as contaminations through fertilizers and pesticides, growing water demand for agriculture and as a response to climate change (Hartmann et al., 2014). In Brazil, karst systems can be found mostly in the Northeast and Southeast regions (Ferreira & Uagoda, 2020). In the Central Western Brazil, this geomorphology occurs in the the Serra da Bodoquena region (Figure 1). Comprised by a 200 km length strip that extends in the north-south direction (Sallun-Filho & Karmann, 2007), Serra da Bodoquena is a remarkable ecosystem located on the southeastern portion of the Upper Paraguay River basin. Moreover, whilst most bedside streams of this drainage, and consequently of the Pantanal, flow of arenitic Cerrado plateaus from the eastern border, this karst system holds one of the largest Mata Atlântica remnants in Mato Grosso do Sul state. The crystallinity of its waters, due the action of the dissolved limestone makes this region known worldwide, becoming one of the most touristic sites in the country, receiving an amount of about 150.000 tourists a year (OTEB, 2020).

In the Western border of Serra da Bodoquena lies the Parque Nacional da Serra da Bodoquena (PNSB; Figure 2). Created in 2000, the PNSB is the single federal conservation unit of integral protection in Mato Grosso do Sul state and its importance reach regional and national scales since: I) belongs to the Cerrado-Pantanal corridor, a large planning unit that seeks to reconcile nature conservation with responsible economic development according to the social characteristics of the region; II) is inserted in the core zone of the Reserva da

Biosfera da Mata Atlântica; III) surrounds the Reserva Indígena Kadiwéu (538.536 hectares); besides, it is a fundamental part of the Reserva da Biosfera do Pantanal, holds watersheds that supplies the region's main hydrographic basins and shelters the largest remnant of deciduous seasonal forest Mato Grosso do Sul state (Brasil, 2021). Thereby, this region is considered an extremely high priority area for conservation according to the Mapa das Áreas Prioritárias para a Conservação, Utilização Sustentável e Repartição de Benefícios da Biodiversidade Brasileira, elaborated by PROBIO and Secretaria de Biodiversidade e Florestas (Brasil, 2007).

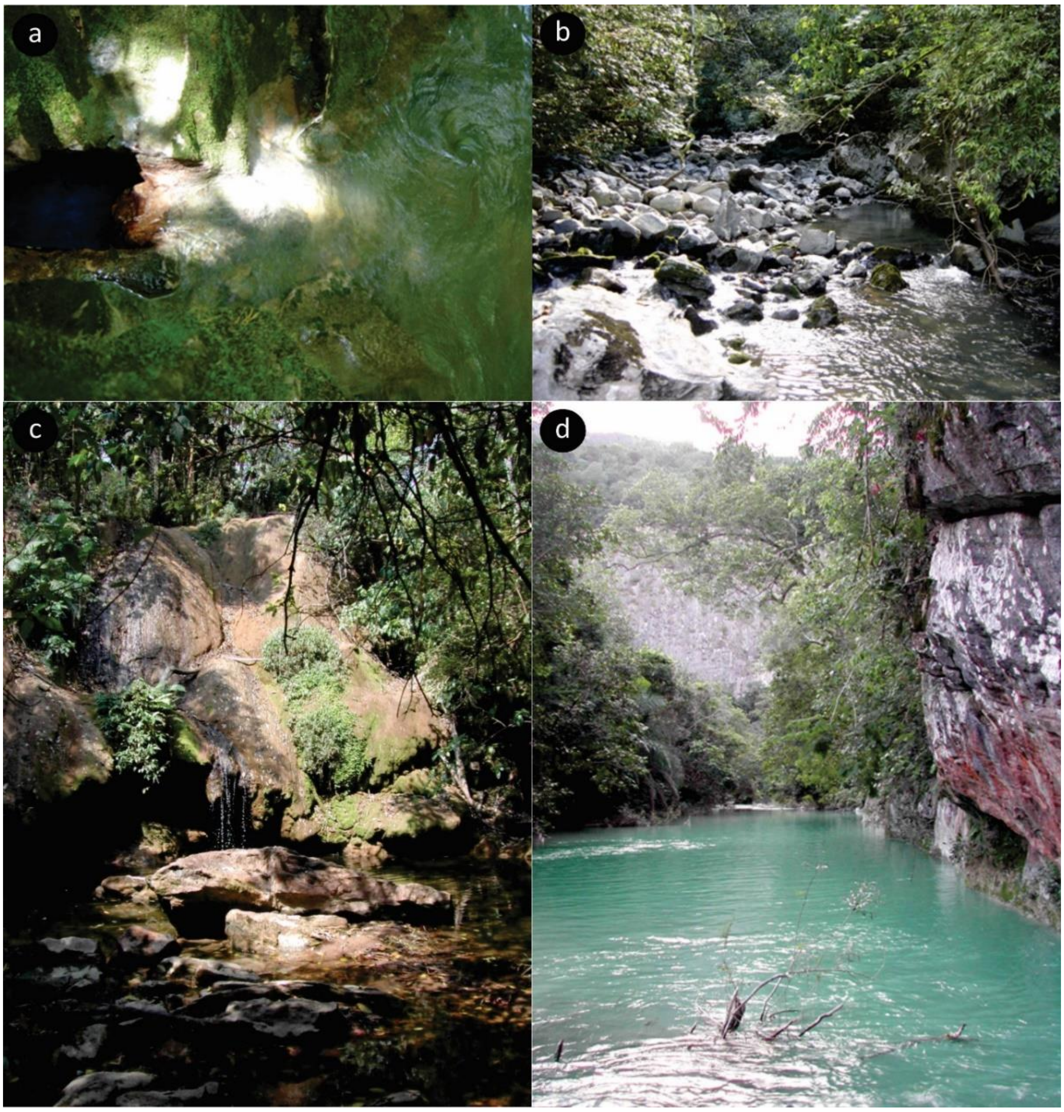

Figure 1 – Typical karst formations in Serra da Bodoquena streams, Western Brazil. A - “Sumidouro” in the Perdido River drainage. B – Ressurgence in Santa Maria stream. C – Formation of limestone “tufas”. D – Rocky wall and riparian forest in the stream surroundings. Source: Extracted from Vilela et al. (2020).

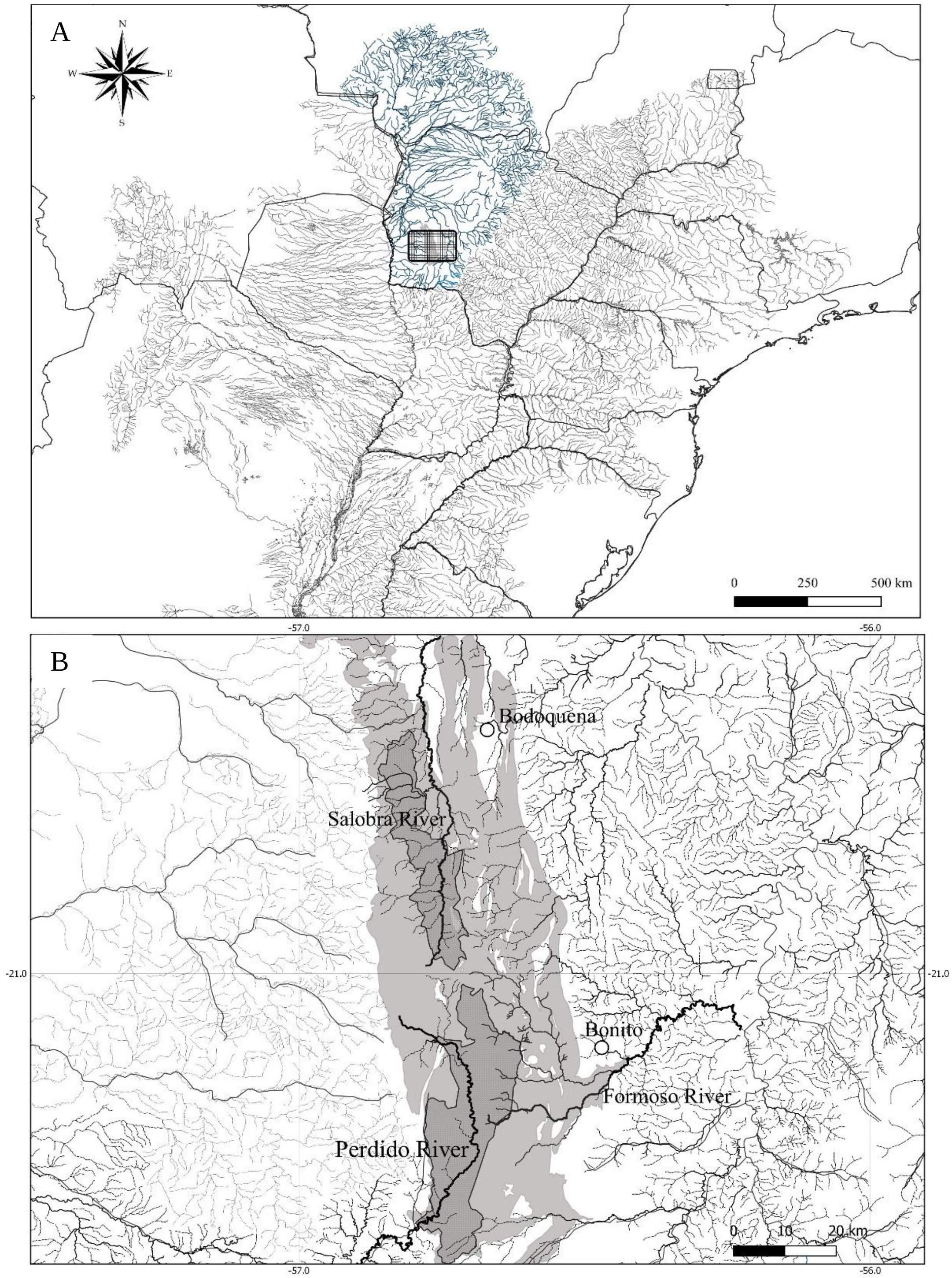

Figure 2. A – Location of Serra da Bodoquena within the Upper Paraguay River basin, the upper drainage of La Plata system. B – Grey area represents the carbonate rocks of Serra da Bodoquena; shaded area the Parque Nacional da Serra da Bodoquena, and the rivers which are focus of this Thesis. Source: Prepared by the author.

The park covers an area of about 76,000 hectares split in two portions, North and South, with distinct geomorphological features. In the North portion, the main drainage belongs to Salobra River, a tributary of Miranda watershed, with the occurrence of rivers carved in canyons, where the western edge of the mountain has steep cliffs and deep and narrow recesses, while the South portion presents a less steep landscape and the main drainage belongs to Perdido river, a tributary of Apa watershed, and springs of Formoso River, also of Miranda watershed. Although these drainages present mostly of its surroundings covered by original savanic and forest formation within the PNSB domains, their extensions are beyond the park limits. Salobra drainage cover an area of 250,000 hectares, Formoso and Perdido drainagens covers 125,000 and 72,000 hectares, respectively (Imasul, 2014). Across their range off the PNSB these rivers suffer the influence of landscape modification to agricultural or pastoral activities, urban effluents, marsh dredging, road crossing, in addition to direct and indirect impacts from the tourism, such as resource consumption, waste generation, infrastructure and acess to natural areas (Bessa et al., 2017).

Upper Paraguay River basin (UPRB) is part of the La Plata-Uruguay-Paraná-Paraguay system, which is the second largest drainage system in South America (Lowe-McConnell, 1987). In terms of fish richness, UPRB holds an amount of 350 fish species (Gimênes-Jr & Rech, 2021), of which 60 are represented in the PNSB (Vilela et al., 2020). However, despite efforts dating back to the year 2000, data about ecology, behavior, distribution, diet and taxomony of this group still incipient in the Serra da Bodoquena as a whole. A reflex of this unrecognized diversity lies on the seven new species described in the region from 2004 to 2021, beyond the undescribed ones from *Ancistrus*, *Astyanax*, *Australoheros* and *Hypostomus* genus, as example. Contrasting to these recent discoveries, human occupation and the land use conversion for livestock dates back to the 60s and the current large remnants of forests are located in steep areas, which makes access difficult (ICMBIO, 2013). In this way, is paramount that effort that intend to acknowledge aspects of fish ecology in the region be done.

One of the most primordial aspect in relation to animal interactions concerns how organisms explore their habitat and use the resources. These data can elucidate interactions from pair of coexisting species (e.g., Freitas et al., 2017) up to the network of a whole community (Montoya et al., 2006) and, regarding to fish, its relations with the land-water interface. One of the most simple and efficient way to obtain this data is through direct observation of the fish in their natural habitat by snorkeling or diving. Although this technique is most employed on marine habitats, it has proven to be an efficient tool on Neotropical freshwater to gather information about: spatial patterns of habitat use (Ceneviva-Bastos et al., 2010; Romero & Casatti, 2012), nucler-follower interactions (Garrone-Neto & Carvalho, 2011; Teresa et al., 2011), activity patterns and feeding behavior (Sabino & Zuanon, 1998) and functional trophic groups (Sazima, 1986; Brejão et al., 2013; Casatti et al., 2001). Indeed, classification of the species within trophic groups represents a useful summarization of resource and habitat use which favours comparison between communities regardless the taxonomic hierarchy (Simberloff & Dayan, 1991). Complementary, data about diet of the species can present a more fine and detailed information over fish and their resource. In a general sense, fish morphology can favor or limit access to different resources (Matthews, 1998), so, the wide range of shapes in the mega diverse ichthyofauna from Neotropics becomes a challenge. Data about diet can unravel patterns of coexistence through the competitive exclusion principle (Zaret & Rand, 1971) and the role of the resource input derived from riparian forests and the effects of its removal (Lobón-Cerviá et al., 2016), as examples. Moreover, diet information brings up quality data about the food web of the ecosystems, which plays a major gap in the case of tropical freshwaters systems (Winemiller et al., 2008).

Notwithstanding the economic, cultural, touristic and biodiversity aspects of this emblematic region, Serra da Bodoquena also presents a unique feature in the Upper Paraguay River basin hydrology. Whilst most of this basin encompass the wide plains of Pantanal floodplain, reaching between 80 and 150 m.a.s.l., Serra da Bodoquena can reach up to 800 m.a.s.l. (Sallun Filho & Karmann, 2007). This feature contributes to the presence of high flowing streams and, consequently, fish species with adaptations to inhabit high flowing habitats. In a general sense, this kind of environmental restriction, associated with structural elements of the stream, acts as a filter of species in a way that the fish composition is expected to be heterogeneously distributed along the water course (Poff, 1997). Moreover, land use in the streams' surroundings can influence the local composition and represents an additional filter to the community. The environmental filter acts to prevent species that do not have a certain set of characteristics from persisting under a particular set of environmental conditions, so it is considered one of the mechanisms that, together with the limiting similarity, dispersal and colonization-extinction of species, can explain the formation of the assemblages (Sobral & Cianciaruso, 2012).

The variation in species composition between communities in different locations is known as beta diversity (Whittaker, 1960). Beta diversity patterns can be generated by species turnover or richness difference, with nestedness being a special type of the latter (see Legendre, 2014). Turnover is interpreted as the exchange of species in an ecological gradient, due to environmental filters, limited dispersion or historical factors (Benone & Montag, 2021). Richness difference is the difference in the number of species between communities, which may be the result of uneven in the availability of niches or barriers to dispersal (Benone & Montag, 2021). However, the taxonomic facet is only one of those considered in the study of local and/or regional biodiversity, since there is a functional and phylogenetic facet (Cardoso et al., 2014; Pool et al., 2014). Beta functional diversity indicates the variation of functional types between different communities and can be decomposed analogously to taxonomic beta diversity, that is, into turnover and nestedness (Villéger et al., 2013).

In this sense, this Thesis aims to bring up information about habitat use, trophic interactions and distribution patterns of fish from Serra da Bodoquena streams. More specifically, it relies on data collected from streams of Salobra, Formoso and Perdido watersheds, within and outside de PNSB boundaries, in different conditions of habitat integrity. In the first chapter, we explore the habitat use and food acquisition of fish, through direct observations of the individuals on snorkeling sessions in Serra da Bodoquena streams. These aspects of basic natural history are the first step to understand the auto ecology of the species and subside their conservation in a long-term. The second chapter approaches the trophic interactions between fish and their resources and the effect of these interactions in the architecture of the local food web. In conclusion, from the landscape perspective, the chapter three approaches the species distribution and the effects of land use and elevation on the functional and taxonomic beta diversity. In another words, how and whether the landscape influences the fish composition and shape along altitudinal and deforestation environmental gradients.

1.1 References

Bessa E, Silva F, Sabino J. 2017. Impacts of fish tourism. In DT Blumstein, B Geffroy, DSM Samia & E Bessa (Eds.), Ecotourism’s promise and peril (pp. 59–72). Cham, Switzerland: Springer International Publishing AG.

Benone N, Montag L. 2021. Métodos quantitativos para mensurar a diversidade taxonômica em peixes de riachos. Oecologia Australis, 25(2), 399–415.

Brasil. 2007. Ministério do Meio Ambiente. Biodiversidade Brasileira: avaliação e identificação de ações prioritárias para a convervação, utilização sustentável e repartição dos benefícios da biodiversidade Brasileira. Brasília, MMA, Secretaria de Biodiversidade e Florestas.

Brejão GL, Gerhard P, Zuanon J. 2013. Functional trophic composition of the ichthyofauna of forest streams in eastern Brazilian Amazon. Neotropical Ichthyology, 11(2), 361–373.

Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PA, Podani J, Schmera D. 2014. Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. Journal of Biogeography, 41, 749–761.

Casatti L, Langeani F, Castro RMC. 2001. Peixes de riacho do Parque Estadual do Morro do Diabo, Bacia do Alto Rio Paraná, SP. Biota Neotropica, 1, 1–15.

Ceneviva-Bastos M, Casatti L, Rossa-Feres DC. 2010. Meso and microhabitat analysis and feeding habits of small nektonic characins (Teleostei: Characiformes) in Neotropical streams. Zoologia: an international journal for Zoology, 27: 191–200.

Ferreira CF, Uagoda RES. 2020. Um panorama sobre mapeamentos de dolinas no Brasil, feições elementares do carste. Revista Brasileira de Geografia Física, 13(1), 302–321.

Ford DC, Williams PW. 2007. Karst Hydrogeology and Geomorphology, Wiley, Chichester.

Freitas TMS, Montag LF, Barthem RB. 2017. Distribution, feeding and ecomorphology of four species of Auchenipteridae (Teleostei: Siluriformes) in Eastern Amazonia, Brazil. Iheringia, Série Zoologia, 107, e2017008.

Garrone-Neto D, Carvalho LN. 2011. Nuclear-follower foraging associations among Characiformes fishes and Potamotrygonidae rays in clean waters environments of Teles Pires and Xingu rivers basins, Midwest Brazil. Biota Neotropica, 11, 1–4.

Gimênes-Jr H, Rech R. 2021. Guia ilustrado dos peixes do Pantanal e entorno. Instituto do Meio Ambiente de Mato Grosso do Sul. In press.

Hartmann A, Goldscheider N, Wagener T, Lange J, Weiler M. 2014. Karst water resources in a changing world: Review of hydrological modeling approaches. Rev Geophys, 52(3), 218–242.

ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade). 2013. Plano de manejo do Parque Nacional da Serra da Bodoquena. Encarte 3 – Análise do PNSB. Available at www.icmbio.gov.br/portal/images/stories/docs-planos-de-manejo/Encarte3_serra_da_bodoquena.pdf

Imasul (Instituto de Meio Ambiente de Mato Grosso do Sul). 2014. Plano de recursos hídricos da bacia hidrográfica do Rio Miranda. Available at http://www.imasul.ms.gov.br/wp-content/uploads/2015/06/Diagn%C3%B3stico-Final-Plano-de-Bacia-Miranda.pdf

Legendre P. 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23(11), 1324–1334.

Lobón-Cerviá J, Mazzoni R, Rezende CF. 2016. Effects of riparian forest removal on the trophic dynamics of a Neotropical stream fish assemblage: Riparian cover and stream dwelling fishes. Journal of Fish Biology, 89, 50–64.

Lowe-McConnell RH. 1987. Ecological studies in tropical fish communities. Cambridge, Cambridge University Press, 382p.

Matthews WJ. 1998. Patterns in freshwater fish ecology. Norwell, Chapman & Hall.

Montoya JM, Pimm SL, Solé RV. 2006. Ecological networks and their fragility. Nature, 442, 259.

OTEB (Observatório de Turismo de Bonito). 2020. Available in <https://otbonito.com.br/?page_id=268>. Acessed in Aug 23 2021.

Poff NL. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of North American Benthological Society, 16, 391–409.

Pool TK, Grenouillet G, Villéger S. 2014. Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. Diversity and Distributions, 20, 1235–1244.

Romero RM, Casatti L. 2012. Identification of key microhabitats for fish assemblages in tropical Brazilian savanna streams. International Review of Hydrobiology, 97, 526–541.

Root RB. 1967. The niche exploitation pattern of the blue-gray gnat-catcher. Ecological Monographs, 37, 317–350.

Sabino J, Zuanon J. 1998. A stream fish assemblage in Central Amazonia: distribution, activity patterns and feeding behavior. Ichthyological Exploration of Freshwaters, 8, 201–210.

Sater A. 1996. Milhões de Estrelas. Canção do album Caminhos me levem.

Sallun Filho W, Karmann I. 2007. Geomorphological map of the Serra da Bodoquena karst, west-central Brazil. Journal of Maps, 3, 282–295.

Sazima I. 1986. Similarities in feeding behavior between some marine and freshwater fishes in two tropical communities. Journal of Fish Biology, 29, 53–65.

Simberloff D, Dayan T. 1991. The guild concept and the structure of ecological communities. Annual Reviews of Ecology and Systematics, 22, 115–143.

Sobral FL, Cianciaruso MV. 2012. Estrutura filogenética e funcional de assembleias: (re)montando a ecologia de comunidades em diferentes escalas espaciais. Bioscience Journal, 28, 617–631.

Teresa FB, Romero RM, Casatti L, Sabino J. 2011. Habitat simplification affects nuclearfollower foraging association among stream fishes. Neotropical Ichthyology, 9, 121–126.

Villéger S, Grenouillet G, Brosse S. 2013. Decomposing functional β- diversity reveals that low functional β- diversity is driven by low functional turnover in European fish assemblages. Global Ecology and Biogeography, 22, 671–681.

Vilela MJA, Severo-Neto F, Froehlich O, Carvalho FR. 2021. Ictiofauna do Parque Nacional da Serra da Bodoquena, Mato Grosso do Sul, Brasil: composição e subsídios à conservação. Biotemas, 34(2), 1–23.

Whittaker RH. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs, 30(3), 279–338.

Zaret TM, Rand AS. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology, 52, 336–342.

Chapter 1

(formatting rules follow Neotropical Ichthyology journal)

2 Functional trophic groups of fish fauna in headwater karst streams from Brazilian Midwest

2.1 Introduction

The knowledge of natural history plays a key role on protection and conservation of organisms (Dayton, 2003; Bury, 2006). Through this study area, the intrinsic relationships of the animals within their natural habitats can be useful to determine: populations demography, nature and geography of genetic and phenotypic variations, interactions with the environment and other species, priority areas for conservation and enhance the cultural value of animals to human welfare (Greene, Losos, 1988). Although the discipline of natural history dates back to the 18th century (Arnold, 2003), the high diversity of organisms worldwide makes this understanding a difficult challenge. This is especially true considering freshwater ecosystems. Although these habitats represent 0.01% of the world´s surface, they harbor one-third of all living vertebrate species, being the majority of it composed by Neotropical fish fauna (Balian *et al*., 2007). However, fish are not homogeneously distributed in this region, neither the studies about them. In terms of stream-dwelling fishes, knowledge in Upper Paraguay basin, especially in Pantanal and boundaries, still incipient (Lima *et al*., 2021).

Fish species presents a wide range of morphology diversity which implicates on habitat use and food acquisition. A usual tool to the knowledge of trophic positions on assemblage consists on the classification of the species based on simplifying and synthesizing dietary information of organisms on trophic guilds. According to Root (1967), guild is defined as ‘a group of species that exploit the same class of environmental resources in a similar way’. Trophic guilds have proven to be useful in describing the functional roles of species within ecosystems (Franco *et al*., 2008), identifying species most likely to compete for food resources (Specziár, Rezsu, 2009), simplifying complex food webs (Garrison, Link, 2000) and facilitating comparison across systems (Elliott *et al*., 2007). As trophic guilds are useful on understand which resources are consumed, the functional trophic group (FTG) aims to identify how the resources are captured by the animals (Brejão *et al*., 2013). The classification of the species in FTGs summarize behavioural and food acquisition aspects and sheds light on natural history aspects of the community bring on valuable data about the interaction of the organisms in their natural habitat, basically through direct observation on diving sessions (Uieda, 1984; Sazima, 1986; Sabino, Castro, 1990; Sabino, Zuanon, 1998; Casatti *et al*., 2001). However, this technique is limited by the water transparency, which makes this method unfavorable in most cases in Neotropics. In this sense, karst environments present the most favorable scenario once the dissolved carbonate contributes to high crystallinity streams. On Central-Western of Brazil is located one of the most extensive continuous karst areas of the country, the Serra da Bodoquena. It consists of a north-south plateau of about 200 km whose waters drains to the Pantanal floodplain, making this region one of the most unique headwaters from Upper Paraguay River basin (UPRB).

As a contribution to the understanding of functional and trophic aspects of fishes from Pantanal headwaters, this study aims to define and characterize the functional trophic structure of the ichthyofauna of streams at the South Brazilian portion of Upper Paraguay River basin, based on direct underwater observation of habit use and feeding tactics *in situ* of fish assemblages from Serra da Bodoquena streams.

2.2 Methods

Study area

The Serra da Bodoquena is situated in the southwest of Mato Grosso do Sul state, in the Central-Western region of Brazil. With a karst formation and whose origin dates back to the Precambrian (Sallun Filho, Karmann, 2007), this region still preserves much of its original vegetation cover intact, especially in the higher areas, where the headwaters of the streams that drain into rivers of the Upper Paraguay River basin are located (ICMBIO, 2013). In the Western border of Serra da Bodoquena is found the Parque Nacional da Serra da Bodoquena

(PNSB). Created in 2000, the park is the single federal conservation unit of integral protection in the Mato Grosso do Sul state. It covers an area of 76,000 hectares, divided in North and South portions, each one harboring a main drainage: in the North portion, the Salobra river and Perdido river, in the South (Fig. 1). Although headwaters of both rivers are outside the PNSB boundaries, their major extension are within the park limits. In relation to flow direction, the Salobra river flows towards North, in direction of Miranda River, its main river watershed; while the Perdido river flows towards South, in direction of Apa river, its main watershed and the South limit of Upper Paraguay River basin. Beyond these two main rivers, the park South portion also harbors the headwaters of Formoso and Prata rivers, both from Miranda basin. In contrast to the rivers inserted within the PSNB, these latter occur in a smoother terrain, being more exposed to anthopogenic effects of economic activities, such as livestock, road crossing, agriculture and tourism.

Although the region is internationally known as a tourist destination due to its crystalline waters, the ecology of the fish that inhabit the region's streams, e.g., trophic, morphological and distributional attributes, is little known. Currently, the pastures for livestock grazing in the region have been gradually replaced by monocultures, especially soybean, which has caused irreversible environmental damage to the streams, such as siltation and contamination by pesticides (Vilela *et al*., 2020).

Underwater observations

Underwater observations of interactions were performed on day and night periods, from 2003 to 2018, totalizing 360 hours of snorkeling, using *ad libitum* and *focal animal* techniques (Lehner, 1999) on ten stream stretches that ranged from 100 to 2,000 m length (Fig. 1). Observations were based in the Miranda River watershed tributaries (Córrego Salobrinha, Rio Salobra, Rio Sucuri, Rio da Prata, Rio Formoso and Córrego Formosinho);

and in the headwaters and main course of Perdido River. During the nocturnal observations, watertight flashlights with red lights were used, to avoid disturbance of the individuals. To each individual or group of individuals, data about day period, position in vertical dimension (water column), horizontal dimension (margin or main channel) and behavioral characteristics were recorded.

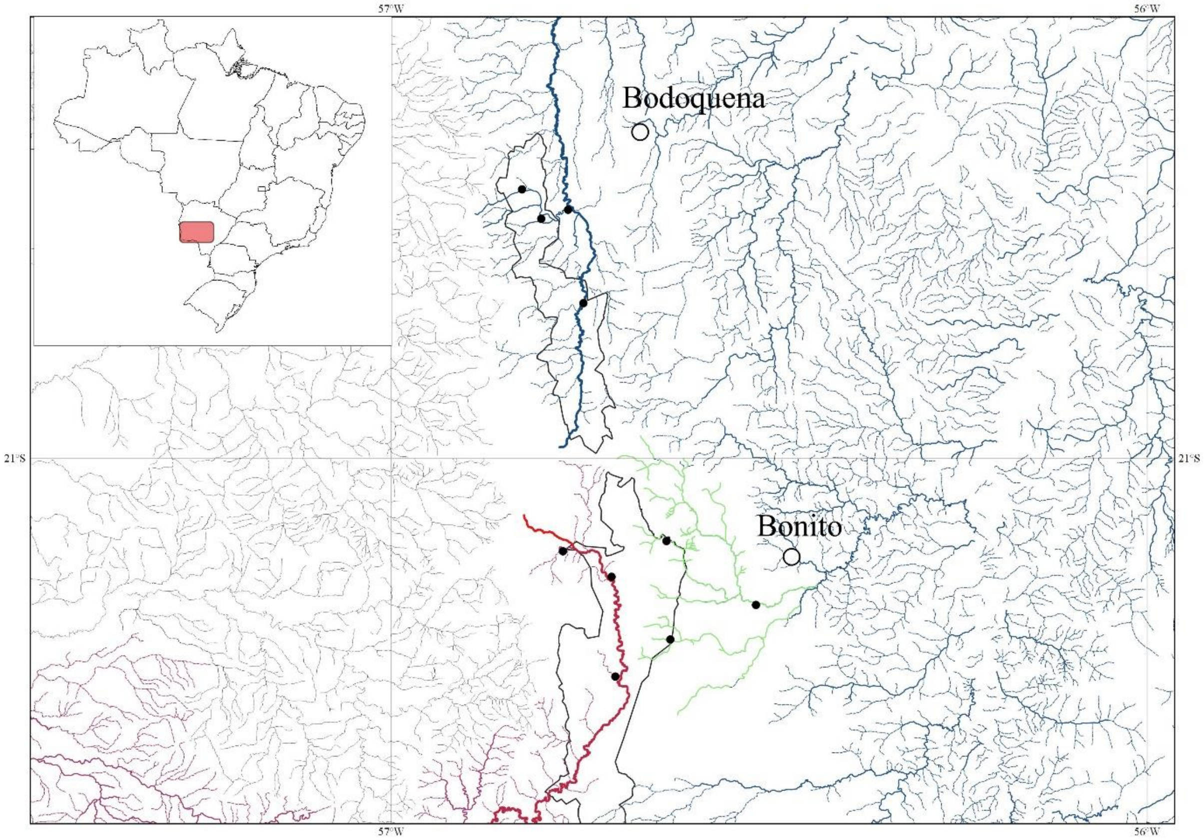

Figure 1 – Main drainages of Serra da Bodoquena: in Blue the Miranda River watershed and in red, Perdido River watershed. Highlighted lines represent Salobra River in the North and Perdido River in the South. In green, Formoso River watershed, a tributary of Miranda drainage. Black dots represent the points of underwater observations of the fish species. Source: Prepared by the author.

In order to verify the body length composition of the community, standard lengths of the species were compiled from Britski et al. (2007), original descriptions of the species or measuring vouchers with digital caliper at Coleção Zoológica da Universidade Federal de Mato Grosso do Sul. Body size classes follow Castro (1999) and Castro, Polaz (2020), in which small species reach up to 15 cm, medium sized those between 15,1 and 44,9 cm, and large those above 45 cm.

Functional Trophic Groups

Classification of functional trophic groups follows Sazima (1986), Sabino, Zuanon (1998) and Brejão *et al.* (2013) according to foraging tactics and habitat use for feeding.

The terms nektonic, nektobenthic and benthic follow the definitions of Lincoln *et al.* (1995): nektonic species are organisms that swim freely in the water column, nektobenthic species are organisms typically associated with the stream bottom that swim actively in the lower portion of the water column, and benthic species are organisms living on, in, or closed associated to the stream bottom.

2.3 Results

A total of 78 species were observed and sampled, being represented by Characiformes with 43 species, followed by Siluriformes (22), Cichliformes (7), Gymnotiformes (3), Cyprinodontiformes (1), Beloniformes (1) and Synbranchiformes (1). The community is based majorly on small species (N=51, 65%), followed by medium sized (N=19, 25%) and large species (N=8, 10%). In terms of horizonal stratification, no significative difference was found between the richness of margin and main channel habitats. However, marginal habitats were occupied by small (up to 15 cm) fish species (Fig. 2).

The ichthyofauna was composed mainly by nektonic (N=35; 45%), followed by benthic (N=26; 33%) and nektobenthic species (N=17; 22%). Sixteen feeding strategies were used by the species (Table 1 of the Supplementary Material) and are described below. The richest feeding tactics were Diurnal Backwater Drift Feeder, with 20% of the richness

(N=16); followed by Grazers, with 14% of the species (N=11) and Crepuscular to Nocturnal bottom predators (9 species, 11%). Characiformes showed the highest amount of feeding tactics with 11 modes, followed by Siluriformes, with four modes.

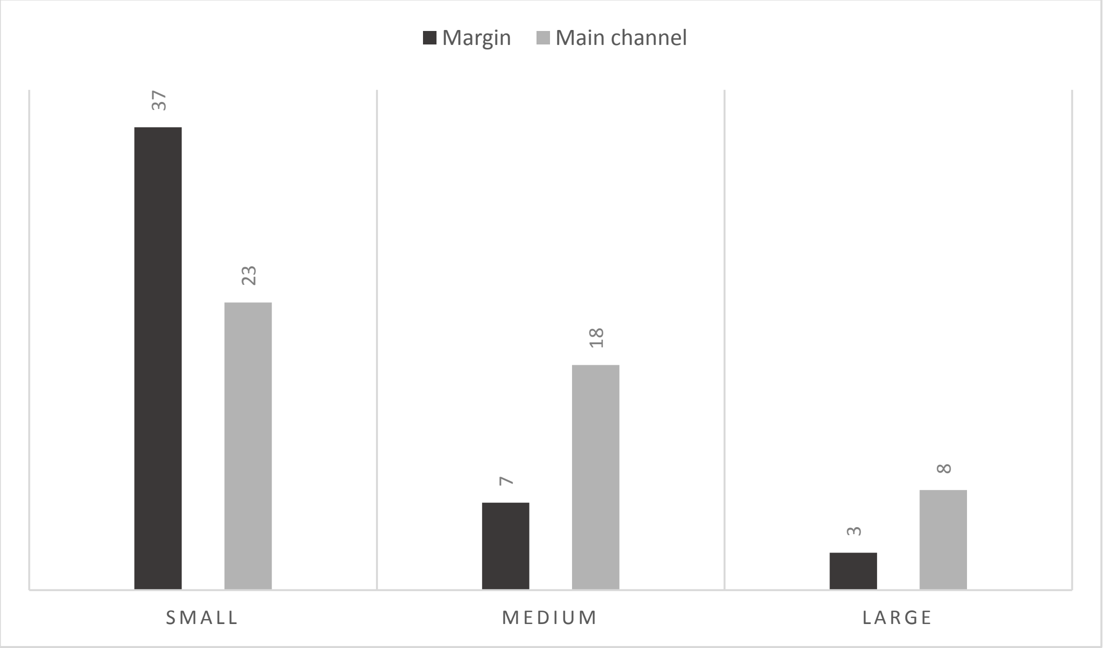

Figure 2 – Distribution of sizes classes of fish from Serra da Bodoquena stream according to instream horizontal occupation. Font: Prepared by the author.

Functional Trophic Groups

Diurnal channel drift feeders: Nektonic species that occupy mostly the main channel during the day foraging on food items drifting at the surface or mid-water (Sazima, 1986; Casatti *et al*., 2001; Brejão *et al*., 2013). This FTG was composed mainly by laterally flattened body, small to medium sized tetra species and “piraputangas” *Brycon hilarii*, which forage actively on drifting food or items fallen from the nearby forest canopy, such as insects, flowers, fruits or leaves. The most abundant species, *Astyanax lineatus*, occurred on conspecific shoals up to 50 individuals investing on items from bottom to surface of the streams, especially on shaded areas or next to fallen logs; *Astyanax abramis* and *A. lacustris* (Fig. 3D) occurred on mixed shoals from mid water to surface. *Astyanax marionae* was the less common of the genera, occurring alone or in small shoals from up to 5 individuals near the margins (Fig. 3G). *Astyanax* sp. 1 occurred on midwater of slow speed runs. *Brachychalcinus retrospina* was the only tall-bodied species of this FTG, and occurred on small groups of 5-10 of its conspecifics along small pools after waterfalls; *Brycon hilarii* was the larger species of this FTG and occurred from mid water to surface, investing on items that fall from the riparian forest, or even jumping out of water to pick fruits from low level branches of the trees. *Bryconops melanurus* occurred on shoals of up to 10 individuals rovering close to water surface and actively capturing insects and fruits that felt from nearby riparian forest.

Diurnal backwater drift feeder: Nektonic fish species that occur close to margins on backwaters and forage on items suspended in the water column or close to the substrate (Sazima, 1986; Casatti *et al*., 2001). Small fishes with laterally flattened body belonging to Characidae family occurring mainly on mixed shoals, associated to roots or submersed macrophytes. *Hyphessobrycon eques* (Fig. 3E) and *Moenkhausia bonita* are the most conspicuous species on Salobra drainage due its remarkable colors and can be found next to margins. *Aphyocharax anisitsi* and *Bryconamericus exodon* are active swimmers that could be observed together next to the margins and whose feeding was based on autochthonous items. *Jupiaba acanthogaster* (Fig. 3E), *Psellogrammus kennedyi* and *Moenkhausia oligolepis* were usually observed on shoals of about 20 individuals, using mid-water to surface areas. *Phenacogaster tegatus* and *Poptella paraguayensis* occurred with small shoals of conspecifics of up to six individuals and presented a stationary behaviour, investing on items sinking or in the surface. *Hemigrammus lunatus* was the less common tetra species, occurring on shaded areas after or before riffles, next to margins. *Piabarchus analis* and *P. torrenticola* occurred on conspecific shoals on shallow areas, next to fallen logs or roots. *Xenurobrycon macropus* was observed always in conspecific shoals up to 40 individuals, swimming on mid-water to surface, along the margin of vegetation belts. *Creagrutus meridionalis* occurred on shoals of up 30 individuals on sandy patches of low flowing current (Fig. 3C). *Astyanax* sp. 2 and *Hyphessobrycon luetkenii* were the two tetras of this FTG found on Perdido River drainage, especially on calm water with dense vegetation near the margins.

Diurnal surface pickers: Species that swim near the surface, especially on backwaters, picking floating organisms or particles of organic debris (Sazima, 1986). Group formed by Lebiasinidae, Poeciliidae and Characidae small species that occupy shallow high densed vegetated margins and fed on invertebrates and debris. *Pyrrhulina australis* was observed usually alone, next to surface on marginal habitats, swimming between the branches or roots of aquatic plants. The guppy, *Poecilia reticulata*, despite being an exotic species on the studied ecosystem, could be observed on impacted drainages, such as urban stretches of the stream, where it occupies shallow pools next to margins, picking debris on the water surface.

Surface strikers: Species that occupy the uppermost layer of the water column, capturing fast and actively mostly invertebrates fallen from the riparian forest (Goulding, Carvalho, 1984; Brejão *et al*., 2013). Group formed by the small nektonic Gasteropelecidae *Thoracocharax stellatus* and the Belonidae *Potamorrhaphis eigenmanni*. The first one presents hypertrophied fins and expansion of the coracoid bone, such as observed on *Carnegiella* species, an Amazon morphologically equivalent species. *Thoracocharax stellatus* was observed on both night and day, moving from margins to the main channel and attacking invertebrates on the surface. *Potamorrhaphis eigenmanni* was observed alone or in five individuals’s shoals, gently rovering near the surface and striking fallen invertebrates or small fish species, as *Xenurobrycon macropus*.

Ambush and stalking predators: Nektonic or nektobenthic species that ambush and/or stalk prey (Sazima, 1986; Sabino, Zuanon, 1998). Group with medium sized representants from two orders (Characiformes and Perciformes) and three families (Erythrinidae, Serrasalmidae and Cichlidae). *Hoplerythrinus unitaeniatus* and *Hoplias malabaricus* were observed stationary on the bottom near the margins ambushing preys on twilight and at night. *Serrasalmus marginatus* could be observed alone during the day, faced towards the prey, hiding its presence by the elongated shape matching submersed branches and roots. The cichlids *Crenicichla lepidota* and *C. vittata* usually used backwaters, transiting between the margins near the bottom and foraging on small fishes or invertebrates after ambushing them; *C. vittata* was more common near the beginning or ending of riffles.

Nibblers: Nektonic fishes that forage through picking and biting food items on solid substrates (Sazima, 1986). Group formed by medium and large sized headstanders Anostomidae *Leporinus*. *Leporinus friderici* occupied midwater to bottom of the water column, occurring with conspecifics or together to *Prochilodus lineatus* shoals, picking fragments of fruits or invertebrates in the bottom or cutting small pieces of aquatic macrophytes. *Leporinus striatus* occurred alone in the bottom, exploring the bottom and margins, picking invertebrates between the rocks of the substrate.

Browsers: Nektonic fishes that bite off small pieces of plants (Sazima, 1986). Group represented by small Cheirodontinae species. Although they have not been observed eating plants exactly, *Odontostilbe pequira* and *Serrapinnus calliurus* formed large mixed shoals, foraging on filamentous algae on roots or rocks surface or in high clusters of algae of about 3 meters that grows from the bottom to the surface in streams with small flow.

Diggers: Species that actively dig the substrate feeding on bottom organisms (Sazima, 1986). Group formed by the small Loricariidae benthic species *Hemiodontichthys acipenserinus*, which occurred on sand patches of the streams bed at night, using its laterally expanded snout to dig in the substrate and stir it looking for benthic organisms.

Pursuit predators: Nektonic species that capture preys through pursuing (Brejão *et al.*, 2013). Group formed by small to large Characidae fishes with elongated, torpedo like bodies. *Acestrorhynchus pantaneiro* and *Oligosarcus perdido* occurred alone or in conspecific shoals next to margins, attacking small fishes next to the surface in the direction of the main channel. *Aphyocharax dentatus* was usually associated to runs, occurring alone or in 4-6 individuals and attacking fish even half of its size; piscivory of this species was demonstrated by Corrêa *et al.* (2009) as well. *Salminus brasiliensis* occurred in the main channel of streams (Fig. 3H); adults usually alone and juveniles in small shoals, even mixed with *Brycon hilarii* adults, an example of predatory mimicry (Bessa *et al.*, 2011).

Mud-eaters: Fish species that ingest soft substrate to feed on minute organisms (Sazima, 1986). Groupo formed by the benthic small *Steindachnerina* and the large Nektobenthic *Prochilodus lineatus*. *Steindachnerina brevipinna* and *S. nigrotaenia* are toothless species that occupy the bottom of the water courses in mixed shoals, picking mud on a headstander position on pools and runs, especially over submerged leaf litters. *Prochilodus lineatus* was observed on large shoals of about 50 individuals, occupying the lower half of the water column and always foraging on the ground, over rocky substrate or submerged logs, where they use the numerous tiny teeth implanted in their lips to scrape the surface (Fig. 3I).

Sit-and-wait predators: Benthic species which capture their prey by stalking (Sazima, 1986; Brejão *et al*., 2013). Group formed by two families (Crenuchidae and Synbranchidae) from two different orders (Characiformes and Synbranchiformes). The small *Characidium* species, *C. borellii* and *C.* aff. *zebra,* performs the same foraging tactic of remain stationary over a rock and, faced towards the stream flow, speculate the substrate around moving the head looking for prey (Fig. 3F); while the first one occupies basically the final stretches of shallow riffles, the second species was more distributed over the stream beds. *Synbranchus marmoratus* uses its elongated finless body to move between the interstice of the rocks during the day and, during the crepuscular and the night, was seen putting the head or half the body out of the rocks (similarly to the behavior of marine eels) and waiting for prey to be reachable by its mouth, especially invertebrates and fish.

Grazers: Benthic species that scratch algae from the substrate (Sabino, Zuanon, 1998; Brejão *et al*., 2013). Group formed by small to large benthic species, being mostly represented by Loricariidae species, which presents body adaptations for scraping food, such as dorsally flat body and ventrally oriented mouth. *Hypostomus basilisko, H. froehlichi, H. perdido* and *H.* sp. 2 were the larger grazers observed. These grazers occupied the bottom of pools during the day, on shaded areas or attached upside down on fallen logs; during night they move to shallow areas in order to scratch algae from boulders and limestone slabs (Fig. 3C). *Ancistrus* sp. Occurred on fast flowing habitats, such as rapids or underneath waterfalls, attached to the rocky substrate; although this species could be observed during all day, larger individuals were more active during the night. *Loricaria luciae* and *Rineloricaria lanceolata* occurred on bottom of pools and runs, usually on rocky substrates, matching its color pattern with the natural patches of light and shade of the substrate. The whiptails catfishes *Farlowella paraguayensis* (Fig. 3A), *Rineloricaria parva* and the Hypoptopomatinae *Otocinclus vittatus* occupied mostly soft leaf litter substrates, where the first two mixed their elongated stick form shape with the sticks and branches of submersed plant matter. The unique non-loricariid grazer was the Parodontidae *Parodon nasus* which occupied fast flowing habitats, usually faced towards the current, and using its upper jaw teeth to scratch algae and periphyton on limestone slabs.

Grubbers: Benthic species that feed on bottom animals through substrate probing while moving (Sazima, 1986). Small Callichthyidae species that uses their barbels upon the uppermost layer of the substrate whilst foraging and eventually probing to capture prey. *Callichthys callichthys* and *Corydoras aeneus* were observed on impacted streams where erosive processes increased the amount of sand deposited in the bottom of the streams. *Callichthys* were observed alone during the night next to margins and *Corydoras* occurred on shoals up to 20 individuals during the day, exploring shallow low-flowing habitats.

Nocturnal invertebrate pickers: Nektobenthic species that capture prey close to substrate during the night (Brejão *et al*., 2013). Medium sized Gymnotiformes from Apteronotidae (*Apteronotus caudimaculosus*), Gymnotidae (*Gymnotus carapo*) and Sternopygidae (*Sternopygus macrurus*). These knifefishes move near the margin using smooth movements to scroll between the boulders and logs looking for aquatic invertebrates inside litter banks, such as Odonata and Megaloptera larvae and adult shrimps.

Pickers and browsers: Nektobenthic species that pick and browse food items dispersed on substrate or organic debris, selecting it through gill rakers (Sabino, Zuanon, 1998; Brejão *et al*., 2013). Group formed by small and medium Cichliformes, with daytime activity on low-current and high heterogeneous habitats. The cichlids *Aequidens plagiozonatus, Australoheros* sp., *Bujurquina vittata* and *Cichlasoma dimerus* were observed usually alone or in pairs, stablishing a determined home range near the margins and chasing off other cichlids that came on nearbyes. The non-native *Coptodon rendalli* could be observed on the Perdido drainage, where adult individuals occupied the water column on margins and shoals of juveniles of about 10cm used highly dense vegetated margins picking food on the substrate and between the submerse plants.

Crepuscular to nocturnal bottom predators: This group was represented by night shift species that explore the bottom of the water courses looking for small prey (Sazima, 1986). Group formed by benthic and nektobenthic small to large specimens of catfishes from the families Heptapteridae, Pimelodidae, Pseudopimelodidae, Trichomycteridae, Auchenipteridae and Aspredinidae. *Pseudoplatystoma reticulatum*, the larger representant of this FTG, remained stationary during the day under the belt of floating macrophytes or inside natural formation holes in the ravines, known as “locas”; during the night the individuals move in the bottom of the main channel exploring the environment with its barbels looking for prey, especially benthic fish species or tetras that remains stationary near the margins during the night. Same behavior and habitat use were observed to *Pseudopimelodus mangurus*, whilst this species included invertebrate on its diet, such as Megaloptera larvae. *Imparfinis schubarti* and *Pimelodella taenioptera* (Fig. 3D) move into shoals of up to 20 individuals, rovering for invertebrates between the pebbles using their barbels and investing on substrate when locate them. Although the first species was more associated with fast flowing habitats, *P. taenioptera* could be seen using all mesohabitats, from riffles to pools. *Rhamdia quelen* was observed alone or in small shoals of 5 individuals and, in low density pools near the stream spring, could be observed using the whole water column, capturing even moths or adults of Ephemeroptera in the water surface (Severo-Neto, 2008). *Ituglanis herberti* and *Phenacorhamdia* sp. are reophilic species that necessarily occurred in the interstice of the pebbles under fast flowing mesohabitats, commonly associated to submersed or floating leaf litters. *Bunocephalus doriae* remained stationary during the day on soft mud subtrates and leaf litters, possibly mimicrying leaves with its shape; during the night this species became actively on this same sort of substrate, probing its snout in the substrate eventually to capture small prey, such as Chironomidae larvae. *Tatia neivai* remained stationary during the day, notably inside hollow submerged branches, and actively foraging in the water column during the night, capturing prey from the substrate to surface.

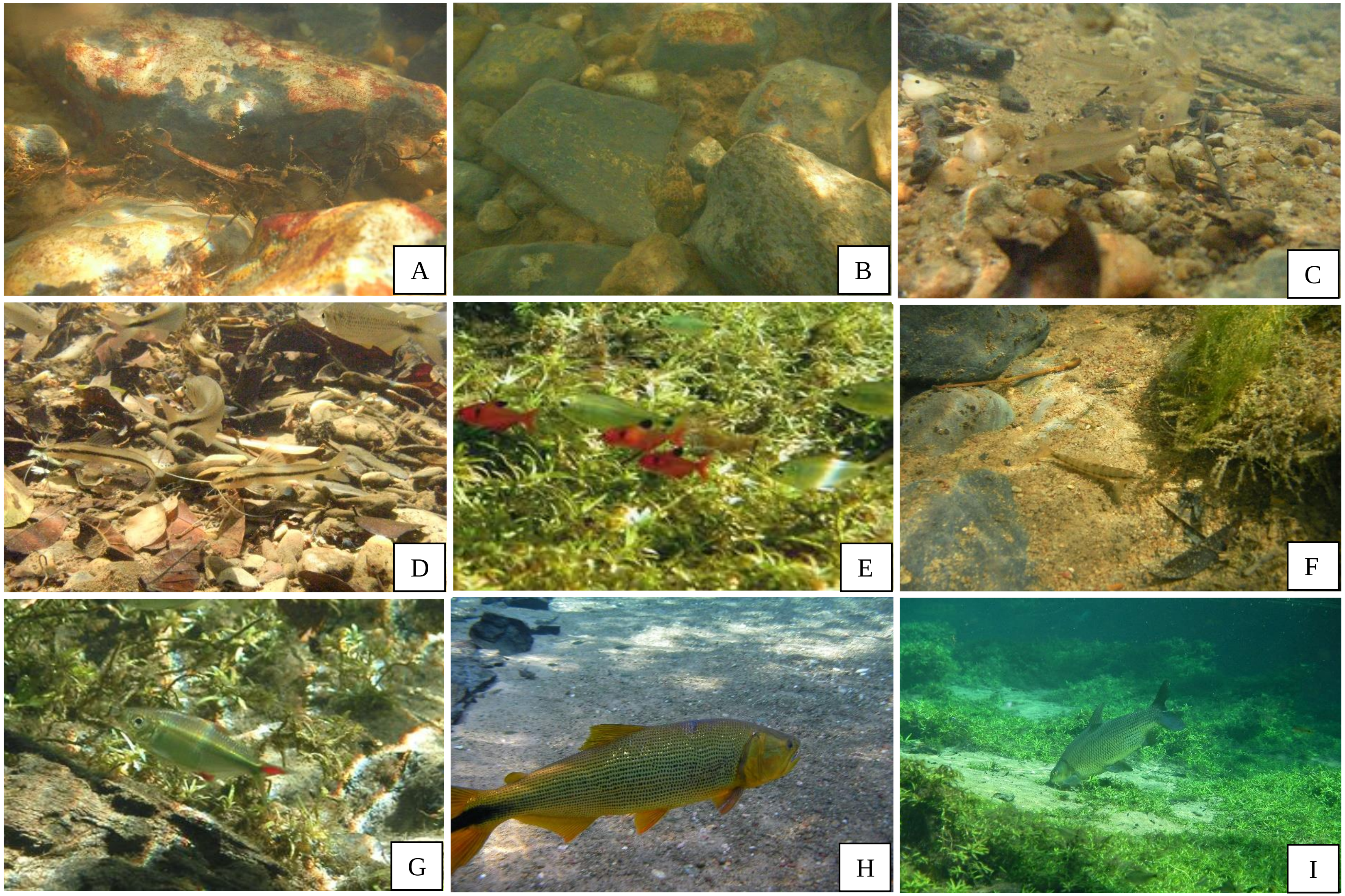

Figure 3 – Representants of the fish assemblage from Serra da Bodoquena streams. A. *Farlowella paraguayensis* between twigs and leaf litter in the substrate; B. *Hypostomus froehlichi* between boulders; C. *Creagrutus meridionalis* foraging near a sandy substrate; D. *Pimelodella taenioptera* and *Astyanax lacustris* foraging among leafs in the substrate; E. *Hyphessobrycon eques* and *Jupiaba acanthogaster* using marginal vegetation; F. *Characidium zebra* using the sit-and-wait tactics on the sandy substrate; G. *Astyanax marionae* foraging near the rocky substrate; H. *Salminus brasiliensis* swimming in the water column; I. *Prochilodus lineatus* foraging near vegetation patches. Photos: Renato M. Romero & Fabrício B. Teresa.

2.4 Discussion

Overall, fish composition from Serra da Bodoquena is composed by small nektonic diurnal backwater drift feeders. This small-sized Characiformes and Siluriformes fish dominance reflects the Neotropical pattern in which around 70% of the more than 4,000 species are under 15cm of standard length (Reis *et al.*, 2003; Castro, Polaz, 2020) and belonging to those two orders (Lowe-McConnell, 1987).

Physical habitat structure is a major factor influencing behavior and ecology of stream fish (Gorman, Karr, 1978). From being a karst system, Serra da Bodoquena presents unique patterns of a set of environmental heterogeneity in the southern portion of Upper Paraguay River basin. Whilst the Pantanal floodplain presents an altitude of about 100 meters and smooth declivity, Serra da Bodoquena reaches from 200 to 800 m.a.s.l (Sallun-Filho, Karmann, 2007). Its altitude range contributes to fast flowing waters that are unlikely in UPRB and, consequently, harbors flow-dependent species, as *Ancistrus*, *Phenacorhamdia* and *Parodon*. The dependence of part of this community to fast flowing habitats can be seen in the convergent morphological traits shared by distant phylogenetic unrelated FTGs species, as the expanded pectoral fins that deflects the water current and anchor the fish to the substrate, as seen in the sit-and-wait predators Crenuchidae, the grazers Parodontidae or the crepuscular to nocturnal predators Heptapteridae. From a microhabitat perspective, the patches of sand, pebbles, boulders and limestone labs in the substrate configure a rich mosaic of foraging and refuge sites to the fish community that are unavailable in the floodplain. The large plain surface area of boulders and limestone labs becomes conducive to the growth of periphyton and algae, which is fundamental to the maintenance of the 15% of the community richness consisted by Loricariidae and Parodontidae grazers. Pebbles acts as perches to sit-and-wait predators to *Characidium* species, from where they observe the surroundings looking for invertebrates, or as foraging sites to Heptapteridae species that actively forages probing between the small rocks. Nonetheless, the small space available between the pebbles works as a predation free corridor to adults of slender catfishes, as *Trichomycterus* and *Phenacorhamdia*, and to Loricariidae fingerlings. Sand patches develop suitable habitats to psammophilous (sand-dwelling) species which representants tend to present a sand-color pattern to remain cryptic with the substrate and sit-and-wait tactics (Zuanon *et al*., 2006). Whilst sand patches are more common near outfalls of the streams due the influence of the sediments carried by the larger floodplain rivers, their presence on higher altitudes streams from Serra da Bodoquena are associated to erosive processes, such as conversion of land to agriculture, urban influence or road construction. Due to this recent and unnatural sand income in the stream beds, no true sand-dwelling species (sand-color pattern and sit-and-wait tactic) were observed in Serra da Bodoquena streams, however these patches were occupied by locally large shoals of *Creagrutus meridionalis* and the benthics *Callichthys callichthys* and *Corydoras aeneus.* Indeed, the presence of *C. aeneus* is considered of loss of environmental quality in this region (Casatti *et al*., 2010).

Riparian forest plays a key role in the aquatic diversity maintenance in the Neotropics (Dala-Corte *et al*., 2020). Serra da Bodoquena streams present a diverse and considerably well-preserved riparian forest with higher vegetation density within the conservation unit boundaries. From the FTGs perspective, the riparian forest provides an income of sticks and leaves that compose the leaf litters where small fish look for refuge or food. Physical elements as tree roots provide shelter to small backwater drift feeder fish species, as well as cover to ambush and stalking predators; fallen trunks become feeding sites to grazers that scrap the algae and periphyton that grows on them, as hollow logs are day shelter to crepuscular to nocturnal bottom predator, as *Tatia neivai*. Notwithstanding with the clear and well-recognized role of riparian forests upon stream-dwelling fish communities, the margins within the water courses represent a fundamental component to fish fauna diversity maintenance.

Considering the instream plant diversity, however Serra da Bodoquena streams present a high richness of aquatic vegetation, with more than 40 species catalogued to region (Scremin-dias *et al*., 1999). These heterogeneous dense vegetated patches configure the habitat of many species that use them looking for shelter and food, especially the small sized ones. Indeed, this group corresponded to 40% of the ichthyofauna of Serra da Bodoquena streams and were almost exclusive to marginal habitats. We acknowledge that the work focus on adult size of the fishes while juveniles of larger fishes can also occupy marginal habitats. However, marginal habitats can consist an integral home range of small fish during their lifetime. The fall of the quality or total loss of this particular environmental can be risk to small fish, which already are the most threatened group of Neotropical ichthyofauna (Polaz, Castro, 2020). Moreover, while streams which are focus of ecotourism activities in the studied region tend to present more conservate margins with strict rules about vegetation trampling, this is not the case to most of streams from Formoso basin, especially those with historical use of livestock activities. In such areas, streams were used as a source of water to cattle which increased the trampling and siltation of the margins consequently and total suppression of aquatic macrophytes.

The results of this capter reinforces the knowledge of natural history aspects of fish fauna to a consequent future management and conservation of stream-dwelling fishes. Data about the species within their natural habitats can help elucidate distribution patterns and microhabitats preference reinforcing *a posteriori* inferences of studies using functional traits. As example, *Rhamdia quelen* and *Tatia neivai* would parsimoniously be categorized as bottom feeders considering only their ecomorphological attributes, however the direct observation could reveal that these species are able to use the whole water column during foraging. Similar consideration can be attributed to *Hemiodontichthys acipenserinus*, a ventrally flattened loricariid fish that uses its snout morphology to probe into the substrate, capturing small organisms. In view of this, the knowledge of natural history aspects of fish fauna in Serra da Bodoquena streams makes a fundamental role to a better comprehension and conservation of this unique set of species from Upper Paraguay River basin.

2.5 References

Arnold SJ. Anniversary essay: Too much natural history, or too little? Animal Beh. 2003; 65:1065–68. https://doi.org/10.1006/anbe.2003.2143

Balian EV, Lévêque C, Segers H, Martens K. The freshwater animal diversity assessment: an overview of the results. Hydrobiol. 2008; 595:627–37. https://doi.org/10.1007/s10750-007-9246-3

Bessa E, Carvalho LN, Sabino J, Tomazzelli P. Juveniles of the piscivorous dourado *Salminus brasiliensis* mimic the piraputanga *Brycon hilarii* as an alternative predation tactic. Neotrop Ichthyol. 2011; 9:351–354. https://doi.org/10.1590/S1679-62252011005000016

Brejão GL, Gerhard P, Zuanon J. Functional trophic composition of the ichthyofauna of forest streams in eastern Brazilian Amazon. Neotrop Ichthyol. 2013; 11(2):361–373. https://doi.org/10.1590/S1679-62252013005000006

Britski HA, Silimon KZS, Lopes BS. Peixes do Pantanal. Manual de identificação. 2ed. 2007. Brasília, Embrapa. 227p.

Bury RB. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. Herpetol Conserv Biol. 2006; 1:56–61.

Casatti L, Langeani F, Castro RMC. Peixes de riacho do Parque Estadual do Morro do Diabo, Bacia do Alto Rio Paraná, SP. Biota Neotrop. 2001; 1:1–15. https://doi.org/10.1590/S1676-06032001000100005

Casatti L, Romero RM, Teresa FB, Sabino J, Langeani F. Fish community structure along a conservation gradient in Bodoquena Plateau streams, central West of Brazil. Acta Limnol Bras. 2010; 22: 50–59. https://doi.org/10.4322/actalb.02201007

Castro RMC, Polaz CNM. Small-sized fish: the largest and most threatened portion of the megadiverse neotropical freshwater fish fauna. Biota Neotrop. 2020; 20:e20180683. https://doi.org/10.1590/1676-0611-BN-2018-0683

Castro RMC. Evolução da ictiofauna de riachos sul-americanos: padrões gerais e possíveis processos causais. Oecol Brasil. 1999; 6(1): 139–55.

Corrêa CE, Hahn NS, Delariva RL. Extreme trophic segregation between sympatric fish species: the case of small sized body *Aphyocharax* in the Brazilian Pantanal. Hydrobiol. 2009; 635:57–65. https://doi.org/10.1007/s10750-009-9861-2

Dala-Corte RB, Melo AS, Siqueira T, Bini LM, Martins RT, Cunico AM, Monteiro-Júnior CS *et al*. Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region. J Appl Ecol. 2020; 57(7):1391–402. https://doi.org/10.1111/1365-2664.13657

Dayton PK. The importance of the natural sciences to conservation. Am Nat. 2003; 162:1–13. https://doi.org/10.1086/376572

Elliott M., Whitfield, A.K., Potter, I., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G. & Harisson, T.D. 2007. The guild approach the categorizing estuarine fish assemblages: a global review. Fish and Fisheries. 8:241-268. doi:10.1111/j.1467-2679.2007.00253.x

Franco A, Elliott M, Franzoi P, Torricelli P. Life strategies of fishes in European estuaries: the functional guild approach. Marine Ecology Progress Series. 2008; 354:219–228.

Garrison LP, Link JS. Dietary guild structure of the fish community in the northeast united states continental shelf ecosystem. Mar Ecol-Prog Ser. 2000; 202: 231–240.

Gimênes-Jr H, Rech R. 2021. Guia ilustrado dos peixes do Pantanal e entorno. Instituto do Meio Ambiente de Mato Grosso do Sul. In press.

Gorman OT, Karr, JR. Habitat structure and stream fish communities. Ecology. 1978; 59(3):507–15. https://doi.org/10.2307/1936581

Goulding M., Carvalho ML. Ecology of Amazonian needlefishes (Belonidae). Rev Bras Zool. 1984; 2:99–111. https://doi.org/10.1590/S0101-81751983000300002

Greene HW, Losos JB. Systematics, natural history, and conservation: Field biologists must fight a public-image problem. BioScience. 1988; 38(7):458–62. https://doi.org/10.2307/1310949

ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade). 2013. Plano de manejo do Parque Nacional da Serra da Bodoquena. Encarte 3 – Análise do PNSB. Available at www.icmbio.gov.br/portal/images/stories/docs-planos-de-manejo/Encarte3_serra_da_bodoquena.pdf

Lehner PN. Handbook of ethological methods. Cambridge: Cambridge University Press; 1996.

Lima LB, Marco Jr P, Lima-Junior DP. Trends and gaps in studies of stream-dwelling fish in Brazil. Hydrobiol. 2021; 848:3955–68. https://doi.org/10.1007/s10750-021-04616-8

Lincoln RJ, Boxshall GA, Clark PF. Diccionario de ecología, evolución y taxonomía. Mexico: Fondo de Cultura Económica; 1995.

Lowe-McConnell R. Ecological studies in tropical fish communities. London/New York: Cambridge University Press; 1987.

Reis RE, Kullander SO, Ferraris CJ, Jr., editors. Check list of freshwater fishes of South and Central America. Porto Alegre: Edipucrs; 2003.

Root RB. The niche exploitation pattern of the blue-grey gnatcatcher. Ecol Monogr. 1967; 37:317–50. https://doi.org/10.2307/1942327

Sabino J, Castro RMC. Alimentação, período de atividade e distribuição espacial dos peixes de um riacho da Floresta Atlântica (sudeste do Brasil). Rev. Bras. Biol. 1990; 50:23-26.

Sabino J, Sazima I. Association between fruit-eating fish and foraging monkeys in western Brazil. Ichthyol Explor Freshw. 1999; 10(4):309–12.

Sallun Filho W, Karmann I. Geomorphological map of the Serra da Bodoquena karst, west-central Brazil. J Maps. 2007; 2007:282–95. https://doi.org/10.1080/jom.2007.9710845

Sazima I. Similarities in feeding behavior between some marine and freshwater fishes in two tropical communities. J Fish Biol. 1986; 29:53–65. https://doi.org/10.1111/j.1095-8649.1986.tb04926.x

Scremin-Dias E, Pott VJ, Souza PR, Hora RC. 1999. Nos Jardins Submersos da Bodoquena: Guia para Identificação das Plantas Aquáticas de Bonito e Região de Bonito/MS. Editora da Universidade Federal de Mato Grosso do Sul.

Severo-Neto F. Análise da alimentação natural de Rhamdia quelen (Siluriformes: Heptapteridae) na Serra da Bodoquena, MS. 2008; Monograph in Biological Sciences. Campo Grande.

Severo-Neto F, Teresa FB, Froehlich O. Ecomorphology and diet reflect the spatial segregation between two Siluriformes species inhabiting a stream of the Bodoquena Plateau, in Central Brazil. Iheringia, Sér. zool. 2015; 105(1):62–68. https://doi.org/10.1590/1678-4766201510516268

Specziár A, Rezsu ET. Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. J. Fish Biol. 2009; 75:247-267. PMid:20738494. doi:10.1111/j.1095-8649.2009.02283.x

Uieda VS. Ocorrência e distribuição dos peixes em um riacho de água doce. Rev Bras Biol. 1984; 44:203–13.

Vilela MJA, Severo-Neto F, Froehlich O, Carvalho FR. Ictiofauna do Parque Nacional da Serra da Bodoquena, Mato Grosso do Sul, Brasil: composição e subsídios à conservação. Biotemas 2021; 34(2):1–23.

Zuanon J, Bockmann FA, Sazima I. A remarkable sanddwelling fish assemblage from central Amazonia, with comments on the evolution of psammophily in South American freshwater fishes. Neotrop Ichthyol. 2006; 4:107–18. https://doi.org/10.1590/S1679-62252006000100012

2.6 Supplementary material

Table 1. Fish species registered in the Serra da Bodoquena streams, their vertical and horizontal position in the water column and Feeding Trophic Groups (FTG).

Taxa	Vertical stratification	Horizontal stratification		FTG
		Margin	Main Channel	
CHARACIFORMES				
Parodontidae				
Parodon nasus Kner, 1859	Benthic		X	Grazer
Curimatidae				
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)	Benthic	X		Mud-eater
Steindachnerina nigrotaenia (Boulenger, 1902)	Benthic	X		Mud-eater
Prochilodontidae				
Prochilodus lineatus Valenciennes, 1836	Nektobenthic		X	Mud-eater
Anostomidae				
Leporinus friderici Bloch, 1794	Nektobenthic		X	Nibbler
Leporinus striatus Kner, 1858	Nektobenthic		X	Nibbler
Crenuchidae				
Characidium borellii (Boulenger, 1895)	Benthic		X	Sit-and-wait predator
Characidium aff. *zebra* Eigenmann, 1909	Benthic	X	X	Sit-and-wait predator
Gasteropelecidae				
Thoracocharax stellatus (Kner, 1858)	Nektonic		X	Surface striker
Characidae				
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	Nektonic	X		Diurnal backwater drift feeder
Aphyocharax dentatus Eigenmann and Kennedy, 1903	Nektonic	X		Pursuit predator
Astyanax abramis (Jenyns, 1842)	Nektonic		X	Diurnal channel drift feeder
Astyanax lacustris (Lütken, 1875)	Nektonic		X	Diurnal channel drift feeder
Astyanax lineatus (Perugia, 1891)	Nektonic		X	Diurnal channel drift feeder
Astyanax marionae Eigenmann, 1911	Nektonic		X	Diurnal channel drift feeder
Astyanax sp. 1	Nektonic		X	Diurnal channel drift feeder
Astyanax sp. 2	Nektonic	X		Diurnal backwater drift feeder

Brachychalcinus retrospina Boulenger, 1892	Nektonic		X	Diurnal channel drift feeder
Brycon hilarii (Valenciennes, 1850)	Nektonic		X	Diurnal channel drift feeder
Bryconamericus exodon Eigenmann, 1908	Nektonic	X		Diurnal channel drift feeder
Bryconops melanurus (Bloch, 1794)	Nektonic		X	Diurnal channel drift feeder
Creagrutus meridionalis Vari & Harold, 2001	Nektonic	X		Diurnal backwater drift feeder
Deuterodon luetkenii (Boulenger, 1887)	Nektonic	X		Diurnal backwater drift feeder
Hemigrammus lunatus Durbin, 1918	Nektonic	X		Diurnal channel drift feeder
Hyphessobrycon eques Steindachner, 1882	Nektonic	X		Diurnal backwater drift feeder
Jupiaba acanthogaster (Eigenmann, 1911)	Nektonic	X		Diurnal backwater drift feeder
Moenkhausia bonita Benine, Castro & Sabino, 2004	Nektonic	X	X	Diurnal channel drift feeder
Moenkhausia oligolepis (Günther, 1864)	Nektonic	X		Diurnal backwater drift feeder
Odontostilbe pequira (Steindachner, 1882)	Nektonic	X	X	Browser
Oligosarcus perdido Ribeiro, Cavallaro & Froehlich, 2007	Nektonic		X	Pursuit predator
Phenacogaster tegatus (Eigenmann, 1911)	Nektonic	X		Diurnal backwater drift feeder
Piabarchus analis (Eigenmann, 1914)	Nektonic	X		Diurnal channel drift feeder
Piabarchus torrenticola Mahnert & Géry, 1988	Nektonic	X		Diurnal backwater drift feeder
Poptella paraguayensis (Eigenmann, 1907)	Nektonic	X		Diurnal channel drift feeder
Psellogrammus kennedyi Eigenmann, 1903	Nektonic	X		Diurnal backwater drift feeder
Salminus brasiliensis (Cuvier, 1816)	Nektonic		X	Pursuit predator
Serrapinnus calliurus (Boulenger, 1900)	Nektonic	X		Browser
Serrasalmus marginatus Valenciennes, 1837	Nektonic		X	Ambush and stalking predator
Xenurobrycon macropus Myers & Miranda Ribeiro, 1945	Nektonic	X		Surface striker
Acestrorhynchidae				
Acestrorhynchus pantaneiro Menezes, 1992	Nektonic		X	Pursuit predator
Erythrinidae				
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	Nektobenthic	X	X	Ambush and stalking predator
Hoplias malabaricus (Bloch, 1794)	Nektobenthic	X	X	Ambush and stalking predator

Lebiasinidae				
Pyrrhulina australis Eigenmann & Kennedy, 1903	Nektonic	X		Diurnal surface picker
SILURIFORMES				
Aspredinidae				
Bunocephalus doriae Boulenger, 1902	Benthic	X		Crepuscular to nocturnal bottom predator
Trichomycteridae				
Ituglanis herberti (Miranda Ribeiro, 1940)	Benthic		X	Crepuscular to nocturnal bottom predator
Callicththyidae				
Callichthys callichthys (Linneaus, 1758)	Benthic	X		Grubber
Corydoras aeneus (Gill, 1858)	Benthic	X		Grubber
Loricariidae				
Ancistrus sp.	Benthic	X	X	Grazer
Farlowella paraguayensis Retzer and Page, 1997	Benthic	X	X	Grazer
Hemiodontichthys acipenserinus (Kner, 1853)	Benthic		X	Digger
Hypostomus basilisko Tencatt, Zawadzki & Froehlich, 2014	Benthic		X	Grazer
Hypostomus froehlichi Zawadzki, Nardi & Tencatt, 2021	Benthic		X	Grazer
Hypostomus perdido Zawadzki, Tencatt & Froehlich, 2014	Benthic		X	Grazer
Hypostomus sp. 2	Benthic		X	Grazer
Loricaria luciae Thomas, Rodriguez, Cavallaro, Froehlich & Castro, 2013	Benthic	X	X	Grazer
Otocinclus vittatus Regan, 1904	Benthic	X		Grazer
Rineloricaria lanceolata (Günther, 1868)	Benthic	X	X	Grazer
Rineloricaria parva (Boulenger, 1895)	Benthic	X	X	Grazer
Pseudopimelodidae				
Pseudopimelodus mangurus (Valenciennes, 1835)	Benthic		X	Crepuscular to nocturnal bottom predator
Heptapteridae				
Imparfinis schubarti (Gomes, 1956)	Benthic		X	Crepuscular to nocturnal bottom predator
Phenacorhamdia sp.	Benthic		X	Crepuscular to nocturnal bottom predator
Pimelodella taenioptera Ribeiro, 1914	Benthic	X	X	Crepuscular to nocturnal bottom predator
Rhamdia quelen (Quoy & Gaimard, 1824)	Nektobenthic	X	X	Crepuscular to nocturnal bottom predator
Pimelodidae				
Pseudoplatystoma reticulatum Eigenmann & Eigenmann, 1889	Benthic		X	Sit-and-wait predator
Auchenipteridae				

Tatia neivai (Ihering, 1930)	Nektobenthic	X	X	Crepuscular to nocturnal bottom predator
GYMNOTIFORMES				
Gymnotidae				
Gymnotus carapo Linnaeus, 1758	Nektobenthic	X	X	Nocturnal invertebrate picker
Sternopygidae				
Sternopygus macrurus (Bloch and Schneider, 1801)	Nektobenthic	X	X	Nocturnal invertebrate picker
Apteronotidae				
Apteronotus caudimaculosus de Santana, 2003	Nektobenthic	X	X	Nocturnal invertebrate picker
CYPRINODONTIFORMES				
Poeciliidae				
Poecilia reticulata Peters, 1859	Nektonic	X		Diurnal surface picker
BELONIFORMES				
Belonidae				
Potamorrhaphis eigenmanni Ribeiro, 1915	Nektonic		X	Pursuit predator
SYNBRANCHIFORMES				
Synbranchidae				
Synbranchus marmoratus Bloch, 1795	Benthic	X	X	Sit-and-wait predator
CICHLIFORMES				
Cichlidae				
Aequidens plagiozonatus Kullander, 1984	Nektobenthic	X		Picker and browser
Australoheros sp.	Nektobenthic	X		Picker and browser
Bujurquina vittata (Heckel, 1840)	Nektobenthic	X		Picker and browser
Cichlasoma dimerus (Heckel, 1840)	Nektobenthic	X		Picker and browser
Coptodon rendalli (Boulenger, 1897)	Nektobenthic		X	Picker and browser
Crenicichla lepidota Heckel, 1840	Nektobenthic		X	Ambush and stalking predator
Crenicichla vittata Heckel, 1840	Nektobenthic		X	Ambush and stalking predator

<u>Chapter 2</u>

(formatting rules follow Environmental Biology of Fishes journal)

3 Trophic structure and trophic network of the fish fauna in karst streams from the Upper Paraguay River basin

3.1 Introduction

Fish trophic ecology harbors fundamental features to the comprehension of important relationships within the species, such as individual specialization (Xia et al. 2020), the role of predation (Navarro et al. 2017), trophic niche breadth (Roughgarden 1972) and niche partitioning of closely related species (Severo-Neto et al. 2015; Silva et al. 2017; Freitas et al. 2017). From the ecosystem perspective, these interactions represent fundamental roles to broader ecological processes, such as nutrient recycling, fish biomass maintenance and the integrity of the trophic web between the water-land interface. The resources used by species can be defined through stable isotopes (Janjua and Gerdeaux 2011), metabarcoding (Casey et al. 2019) or by the classical gut content analysis. Gut content analysis is a standard tool for identifying fish feeding ecology, trophic interactions and seasonal variations (Janjua and Gerdeaux 2011).

Gut content analysis can also be a useful tool to determine broader ecological processes within communities, such as the construction of food webs (Parravicini et al. 2020; Janjua and Gerdeaux 2011; Vander Zanden and Vadeboncouer 2002). The comprehension of these networks, along with trophic interactions and trophic niches, is paramount for ecological studies and fisheries management (Janjua and Gerdeaux 2011; Winemiller et al. 2008) and consequent subsidies to conservation measures, as demonstrated to marine fish species (Eero et al. 2021). Indeed, fish food webs represent a very interesting study subject once this group can occupy multiple trophic levels, consume a broad range of resources and transit between different spatial scales in the patchy heterogeneity of aquatic landscapes (see Winemiller and Jepsen 1998).

Food network architecture can be compartmentalized on two community-level patterns: modularity, in which species interact more among themselves than with species belonging to other modules; and nestedness, as the tendency of the interactions of the most specialist species to be subsets of the interactions of the most generalist species and as the trend of species with fewer interactions (specialists) to interact with subsets of the mutualistic partners of species with more interactions (generalists) (*sensu* Valdovinos 2019). High modularity patterns in food networks increase network stability, retaining the impacts of disturbal in a single module and minimizing impacts over other modules (Krause et al. 2003; Teng and McCann 2004); while nested networks minimize competition and promote the increasal in the number of coexisting species (Bastolla et al. 2009), besides promoting less prone communities to random extinctions (Burgos et al. 2007) and habitat loss (Fortuna and Bascompte 2006). Although these metrics can unravel species interaction from parasites and their hosts (Campião et al. 2015) to worldwide communities (Albouy et al. 2019; Ceron et al. 2019) the understanding of their effects over freshwater fish fauna still unexplored. While most studies focusing on aquatic food webs approach marine reef or temperate lake systems, a major gap on tropical freshwater systems understanding lies on food webs (Winemiller et al. 2008). The megadiverse tropical fish fauna represents a challenge in the comprehension of these networks due to the diversity of possible interactions given by the presence of specialized niches (*i.e.* seed, fruit, scale, fin and mucus feeding) in contrast to simpler temperate environments (Winemiller et al. 2008) and by the large fish diversity by itself.

In Brazil, the knowledge of food networks of stream-dwelling fish is very restricted, in comparison to studies with the same theme in rivers and reservoirs (Uieda and Motta 2007). However, streams represent most of Brazilian hydrology, contributing to majority of species endemism, habitat for specialist fishes and as reproduction site of many species, especially the small ones, which configures the large portion of fishes in Neotropics (Castro and Polaz 2020). The approach of trophic organization aspects and structure and functioning of food webs in streams can reveal fundamental properties of the ecosystem, leading to the understanding of relationships and predicting dynamics (Uieda and Motta 2007). Moreover, small streams represent unique habitats in terms of energetic balance between autotrophy and heterotrophy, which means the input of autochthonous or allochthonous resources, respectively. Since the heavy cover of riparian forests result in low autochthonous primary productivity due the light limitation (Necchi and Branco 1992; Oliveira and Calijuri 1996), a higher dependency of allochthonous items is expected. However, this balance can change from the longitudinal perspective of headwaters to downstream, with the consequent changes in water temperature, Sun exposal and algal productivity increase (Power and Dietrich 2002), along with type of vegetation cover, substrate, topography and rainfall (Uieda and Motta 2007).

Knowledge about stream-dwelling fishes from Upper Paraguay River basin (UPRB) represent a major gap in Brazil (Lima et al. 2020). Although most of this basin is composed by the Pantanal floodplain, whose hydrological dynamics is based mostly on large rivers and seasonally floods, highlands in the Eastern boundaries harbors several small streams that drain to the main Pantanal watersheds. In the Southestern of UPRB is located the Serra da Bodoquena, which consists of a 200km length karst system whose streams drains to Miranda and Apa rivers drainages, two important rivers of Pantanal floodplain. Although this region has an economy based on agriculture and tourism activities (Velasquez et al. 2014), the streams and their riparian forests are most well-preserved, especially those presents within the Parque Nacional da Serra da Bodoquena, the single integral protection conservation unity in the Mato Grosso do Sul state. The region is worldwide known from the crystallinity of the water courses which permits the observation of fishes in their natural habitat. Moreover, fish species richness in these habitats is high. While UPRB harbors 350 fish species (Gimênes-Jr. and Rech 2021), Serra da Bodoquena streams present 78 fish species (see Chapter 1) with 42 of them represented in a single stream (Froehlich 2010). Despite these economic and biodiversity appeals, trophic relation of these species still unclear. So, in view of this, this chapter aims to indetifiy trophic aspects of fish fauna from Serra da Bodoquena streams. More specifically, we ask which resources are consumed and shared between the species, and how these interactions act over modularity and nestedness of the food web. We expect that the high taxonomic richness harbored by the streams is structured in a high degree of nestedness and specialization of interactions, which permits the coexistence of similar niche species. Also, we expect a high degree of modularity of the community, represented as formation of trophic groups, as the response to the very own nature of resources input of streams, with low autochthonous productivity and allochthonous input dependency.

3.2 Methods

Study area

The Serra da Bodoquena is situated in the southwest of Mato Grosso do Sul state, in the Central-Western region of Brazil (Figure 1). With a karst formation and whose origin dates back to the Precambrian (Sallun Filho and Karmann 2007), this region still preserves much of its original vegetation cover intact, especially in the higher areas, where the headwaters of the streams that drain into rivers of the Upper Paraguay River basin are located (ICMBIO 2013). In the Western border of Serra da Bodoquena is found the Parque Nacional da Serra da Bodoquena (PNSB). Created in 2000, the park is the single federal conservation unit of integral protection in the Mato Grosso do Sul state. It covers an area of 76,000 hectares, divided in North and South portions, each one harboring a main drainage: in the North portion, the Salobra river and Perdido river, in the South. Although headwaters of both rivers are outside the PNSB boundaries, their major extension are within the park limits. In relation to flow direction, the Salobra river flows towards North, in direction of Miranda River, its main river watershed; while the Perdido river flows towards South, in direction of

Apa river, its main watershed and the South limit of Upper Paraguay River basin. Beyond these two main rivers, the park South portion also harbors the headwaters of Formoso and Prata rivers, both from Miranda basin. In contrast to the rivers inserted within the PSNB, these latter occur in a smoother terrain, being more exposed to anthropogenic effects of economic activities, such as livestock, road crossing, agriculture and tourism.

Although the region is internationally known as a tourist destination due to its crystalline waters, the ecology of the fish that inhabit the region's streams, e.g., trophic, morphological and distributional attributes, is little known. Currently, the pastures for livestock grazing in the region have been gradually replaced by monocultures, especially soybean, which has caused irreversible environmental damage to the streams, such as siltation and contamination by pesticides (Vilela et al. 2020).

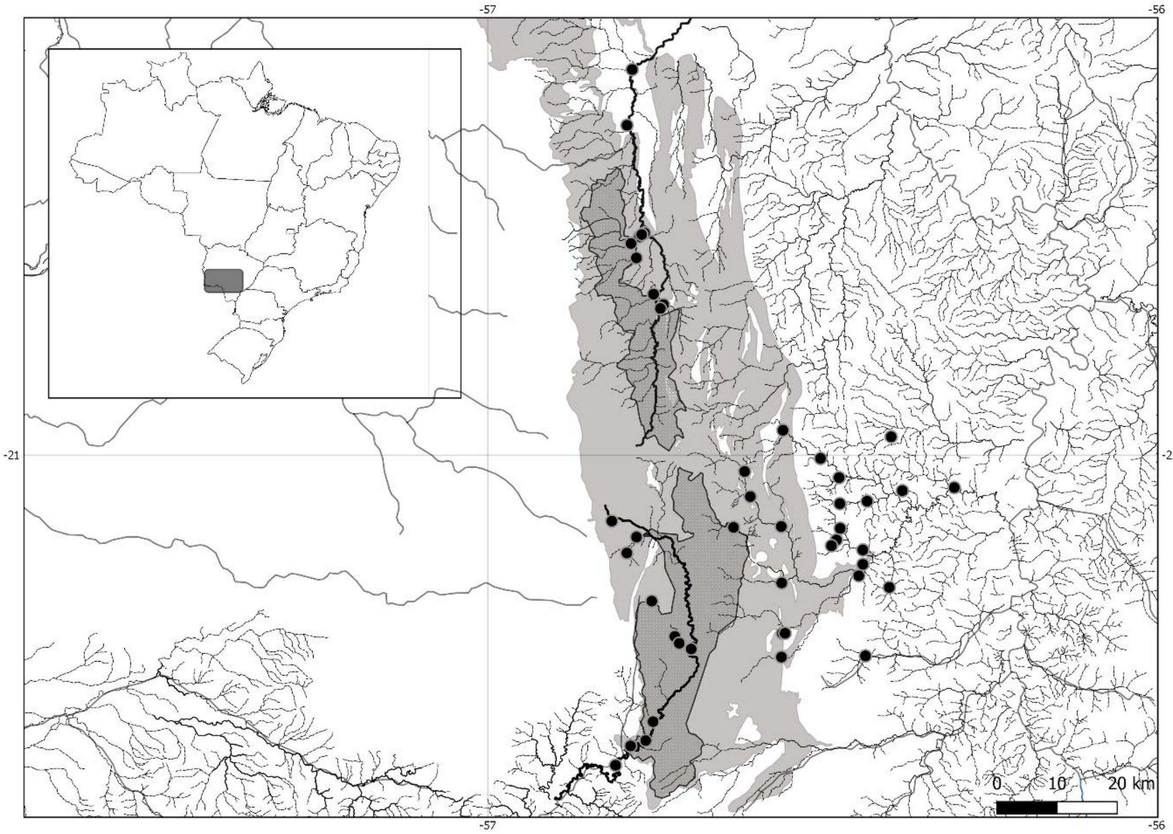

Figure 1 – Location of points of fish collection in Serra da Bodoquena streams. Grey area represents carbonate rocks; Parque Nacional da Serra da Bodoquena in the shaded area. Source: Prepared by the author.

Diet and Trophic Network Analysis

To assess the feeding habitats of the fishes from Serra da Bodoquena, as well as the contribution in the diet of each species, their origin (allochthonous/autochthonous) and the relationships of the mutualistic network, at least five adult individuals of each species deposited at the Coleção Zoológica da Universidade Federal de Mato Grosso do Sul had stomachs content analyzed. In order to reduce the effect of microbasins patterns (Salobra, Formoso and Perdido) and approach the structure of the whole region, fish were selected randomly from the three watersheds. Also, a rarefaction curve using the cumulative of feeding items was provided to each species to determine the degree of reliability of the samples (guts) in the species diet. Items were identified to the lowest possible taxonomic level, as required to the tropic network matrix, and comprehensively classified as allochthonous: allochthonous invertebrates and plant matter; and autochthonous: fish, scales, autochthonous invertebrates, algae and periphyton detritus. To each item, its contribution on the diet of the specimen were assessed by frequency of occurrence (%Fo), measured as the number of times that each item occurs as a percentage of the total number of occurrences of all items (Hynes 1950). Identification of fish species follows Bristki et al. (2007) and original descriptions.

To measure the degree of diet overlap between species, the Morisita-Horn Index was used (CH; Horn 1966, Krebs 1998). CH ranges from 0 (no food items shared) to 1.0 (complete overlap), with values > 0.6 indicating significant overlap (Richard and Wallace 1981). The pairwise relation of food overlap in the fish community was verified through the package spaa (Zhang 2016) in R software (R Core Team 2020).

To improve the comprehension of the interactions between fishes and their diet, we used the relative data on stomach content (food resources consumed) in an approach based on the Theory of Complex Networks (Barabási 2016). For this, interaction matrices **A** were constructed, where a_{ij} = number of interactions of a fish, **i** with prey **j**, and 0 where there are no interactions. For the description of the interactions, we used the following network descriptors: weighted nestedness (wNODF), modularity and complementary specialization (H_2') (Ceron et al. 2019). With these metrics, we intend to access the structure of our network and verify: If diet specialists eat species of a subset of generalist's diet (nestedness); if fishes are grouped into modules according to their diets (modularity) (Parravicini et al. 2020), and; if there are specialists, which eat preferred preys in major degree in relation to the availability of the prey.

Weighted nestedness, based on the Nestedness Metric Based on Overlap and Decreasing Fill (NODF), describes the extent to which interactions of specialist species corresponds to a subset of interaction of generalists (Bascompte et al. 2003). We calculated the weighted nestedness (wNODF), which is based on the overlap and decreasing fill in the weighted matrix (Almeida-Neto and Ulrich 2011). Nestedness values range from 0 (non-nested network) to 100 (perfect nesting). We also calculated modularity, which measures how groups of species are densely connected and present only sparser connections with other groups of interacting species. We analyzed modularity using the recently implemented LPAwb + algorithm (Liu and Murata 2010; Beckett 2016). Finally, we calculated complementary specialization (H_2'), which is a network-wide index of specialization for quantitative interaction matrices. It describes how species restrict their interactions from those randomly expected based on partner's availability (Blüthgen et al. 2006). The assumption is that if species have preferences for specific interaction partners, these preferences would be captured as a deviation from random encounters given by partner availability (Blüthgen et al. 2006). Values of H_2' range from 0 to 1 indicating the extremes of generalization and specialization, respectively. The significance of wNODF, modularity, and H2'were assessed by comparing it with those obtained for randomized networks generated by a null model based on the Patefield´s algorithm (Patefield 1981). We generated 1,000 randomized matrices to estimate nestedness and complementary specialization and 100 matrices to estimate modularity. We used fewer randomizations for modularity because their calculation are time-consuming (Olesen et al. 2007). To quantify the departure of the observed network values from the null expectation, we calculated null- model corrected values by subtracting the observed metric value from the mean value across all randomized networks (Δ – transformation). Then, the Δ – transformed value was divided by the standard deviation of values across all randomized networks (z – transformation; Zanata et al. 2017). All network metrics and null models were calculated with the 'bipartite' ver. 2.08 package (Dormann et al. 2008) in R software (R Core Team 2020).

3.3 Results

In terms of food item consumption, the fish fauna assemblage is basically based on predators of invertebrates, detritivores and piscivores (Figure 2). These three groups also concentrated most of the food overlap pairwise, with 24, 15 and nine species, respectively. Considering the four most frequent items, autochthonous invertebrates was the most consumed item (27%), followed by allochthonous arthropods (21%), detritus (13%) and fish (10%). Autochthonous invertebrates were represented by the aquatical larval stages of Trichoptera, Ephemeroptera, Plecoptera, Diptera, Coleoptera, Odonata, Lepidoptera and Megaloptera, besides Mollusca and Microcrusteacean, while allochthonous invertebrates were adult stages of Hymenoptera, Coleoptera, Lepidoptera, Diptera, Ensifera, Isoptera, Hemiptera and Orthoptera. Allochthonous arthropod were representative (above 50% of frequency of occurrence) in the diet of *Pyrrhulina australis* (Lebiasinidae), *Thoracocharax stellatus* (Gasteropelecidae) and the Characidae *Aphyocharax dentatus, Astyanax abramis, A. abramis,* *A. marionae*, *A.* sp. 2, *Brachychalcinus retrospina*, *Bryconops melanurus*, *Hemigrammus lunatus*, *Moenkhausia bonita*, *Moenkhausia oligolepis*, *Phenacogaster tegatus*, *Piabarchus analis* and *Poptella paraguayensis.*

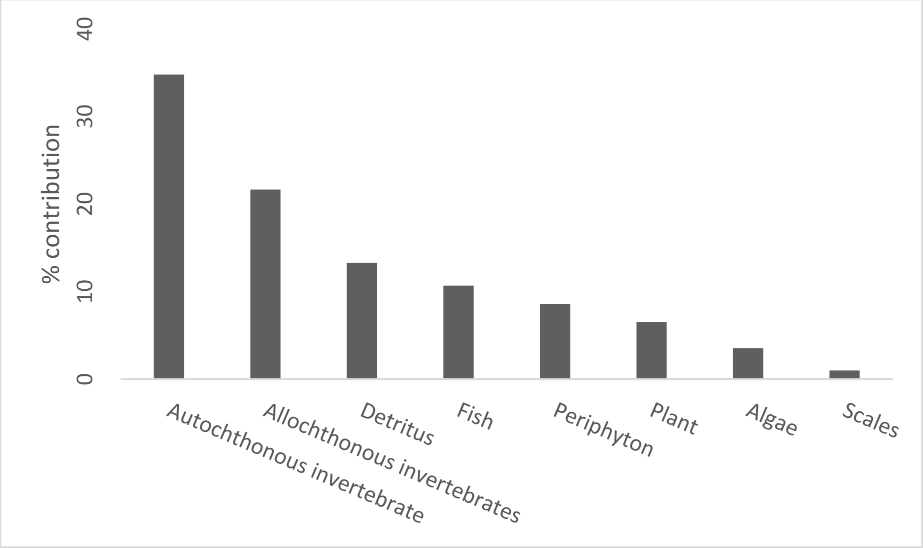

Figure 2 – Resources and their contribution (%) on the diet of fish species from Serra da Bodoquena streams. Source: Prepared by the author.

Trophic web

Fish-diet interactions shown a nested (9.94, $p < 0.01$), high specialized (0.58, $p < 0.01$) and high modular pattern (0.51, $p < 0.01$) (Figure 3). To modularity, as in the cluster categorization, we recovery eight modules according fish-diet interactions. Modules recovery the dietary guild from fishes (Figure 4) and can be grouped as: algivores, periphytivores/detritivores, piscivores, terrestrial insectivores, diptera-larvae feeders, aquatic invertivores, aquatic insectivores, frugivores.

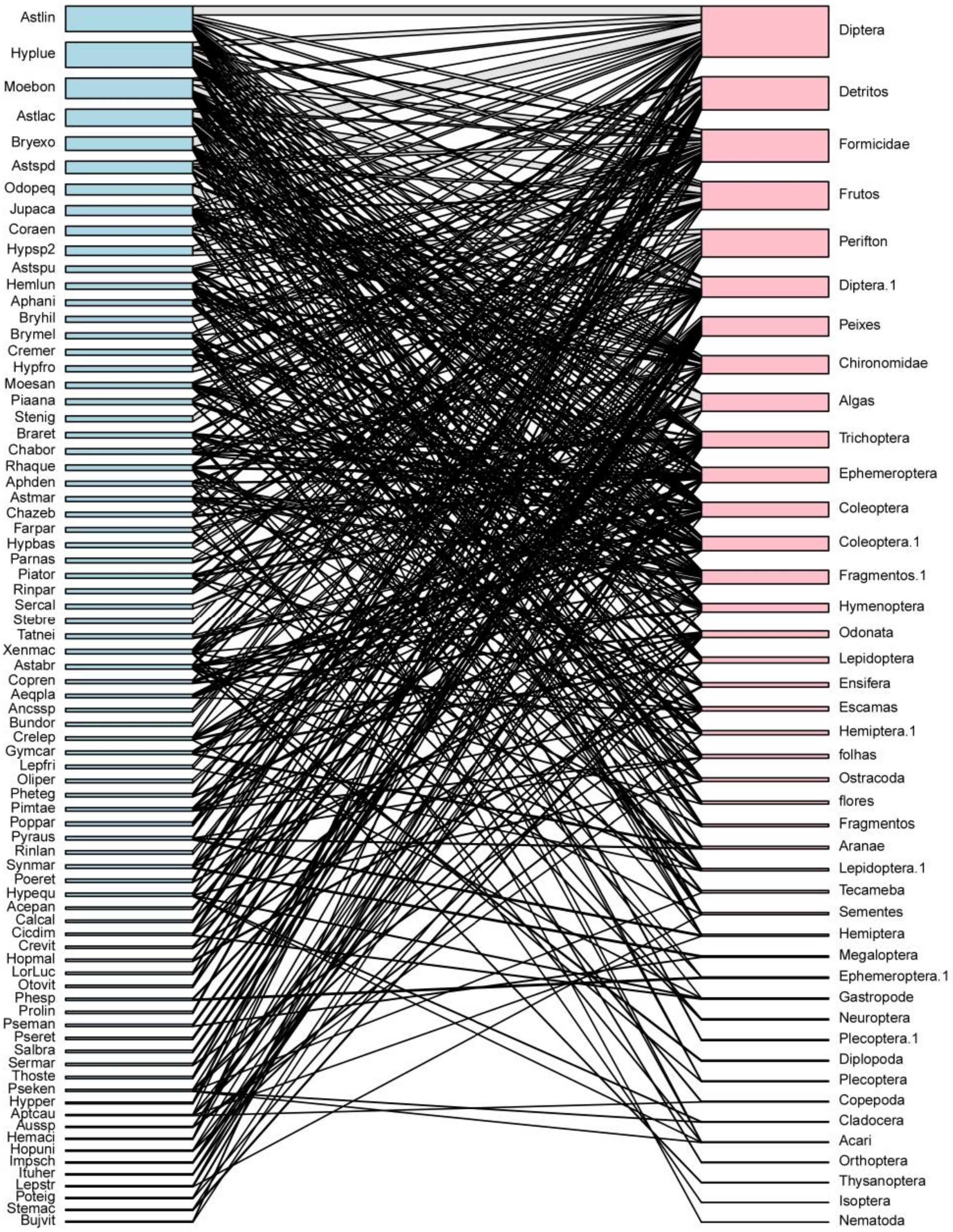

Figure 3 – Interaction network among fishes (blue rectangle) and prey items (pink rectangle) from Serra da Bodoquena streams. See Table 1 in Supplementary Material to species abbreviations. Source: Prepared by the author.

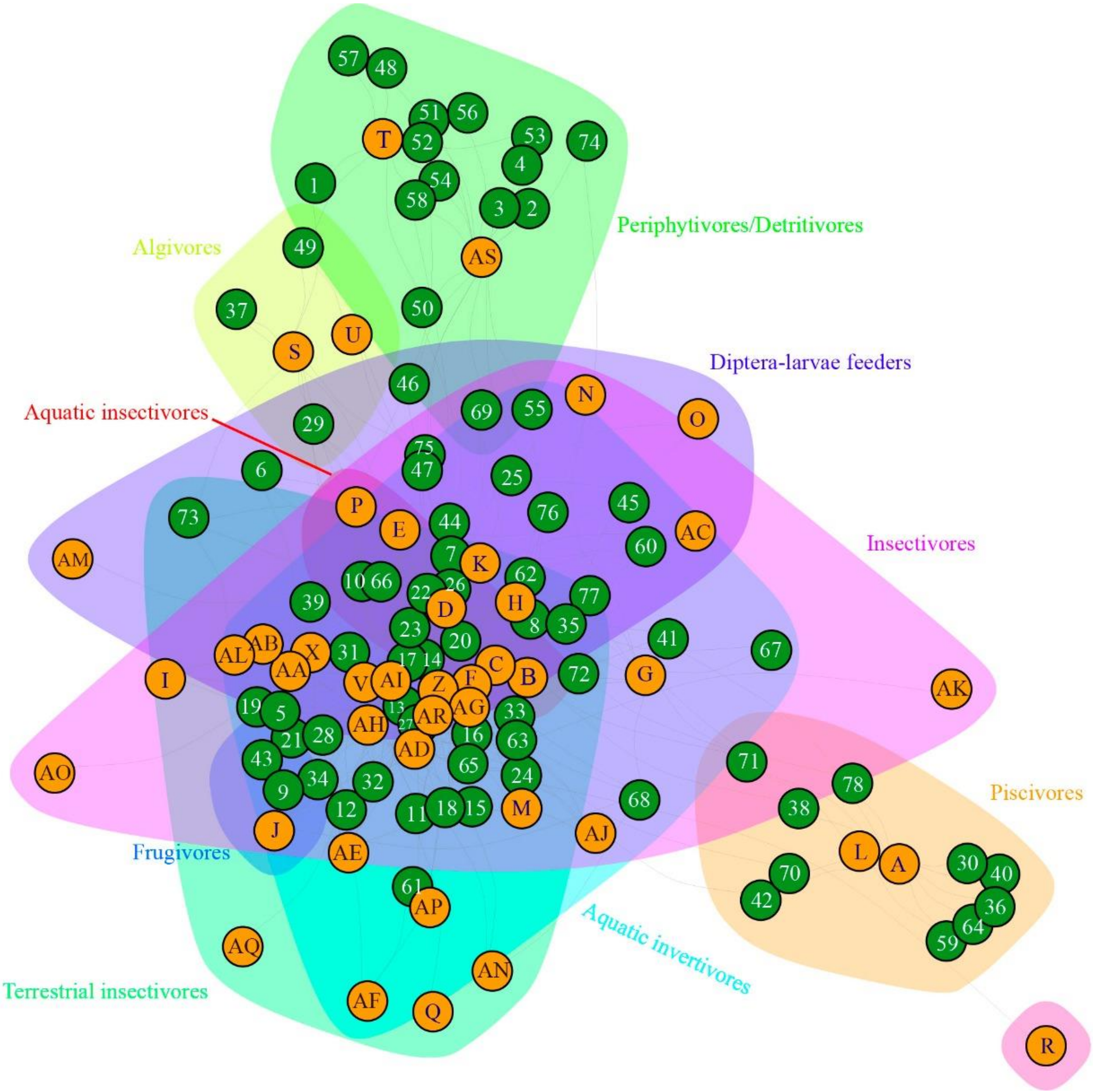

Figure 4 – Species grouped into modules according to fishe's diets, representing trophic guilds, where green circles are fishes species and orange circles are preys. Species and preys codes are presented in the Supplementary material. Source: Prepared by the author.

3.4 Discussion

Autochthonous items represent an important source of resources to streams (Saunders et al. 2018). According to the river continuum concept (Vannote et al. 1980) aquatic primary production is the main energy base in mid-sized streams, in comparison to smaller headwater streams or larger lowland rivers, in which, allochthonous resources prevail. In Serra da Bodoquena, algae and periphyton were the main resources of eleven species, mostly, loricariid armored catfishes. Although algivorous and periphytivores lacks in richness, they represent major part of abundance and biomass in Serra da Bodoquena streams. Indeed, *Ancistrus* sp., the smallest representant of armored catfishes in region, correspond as the second most abundant and, along with *Hypostomus basilisko* and *H. froehlichi*, to almost 40% of total biomass in Salobrinha stream (Froehlich 2010). Moreover, algae and periphyton, are the basis to the maintenance of shredders and scrapers macroinvertebrates, as Ephemeroptera, Plecoptera and Trichoptera orders. Which, in turn, represents the main item to twenty-two species, especially those associated with substrate, such as *Characidium*, *Phenacorhamdia* and *Pimelodella*. A potential threat to these mutualistics networks comes from the trampling caused by tourist in the region, which, affects the macroinvertebrate community, especially Ephemeroptera and Trichoptera (Escarpinati et al. 2014). However, such impact was not evident over smaller body size insects, such as Diptera larvae, which played a major role on the community modularity. Consumption of this item, especially Chironomidae, was high for "lambaris" as *Aphyocharax* anisitsi, *Astyanax* spp., *Hemigrammus lunatus*, *Hyphessobrycon eques*¸ *H. luetkenii*, *Jupiaba acanthogaster* and *Moenkhausia bonita*. While the high dominance of Chironomidae can be considered of an indicative of habitat degradation (Ruaro et al. 2016) the secondary production promoted by these insects is related as key to maintenance of fish abundance on Northern hemisphere streams (Berg and Hellenthal 1992) and its role over Neotropical food webs is still uncertain. However, our results reinforce this source of autochthonous item as fundamental to fish diversity in Serra da Bodoquena streams.

Riparian forest plays a key role in the aquatic diversity maintenance in the Neotropics (Dala-Corte et al. 2020) Serra da Bodoquena streams present a diverse and considerably well-preserved riparian forest with higher vegetation density within the conservation unit boundaries. From the structural perspective, the riparian forest provides an income of sticks and leaves that compose the leaf litters where small fish look for refuge or food. This organic matter patches are paramount to the maintenance of detritivorous/iliophagus, which are few in the region of Serra da Bodoquena (N=3) when compared to fish assemblages from Pantanal floodplain (N=17, Pereira and Resende 1998) where there is greater availability of detritus in the river substrates.

In general, low order streams, *i.e.*, first to third order, depends mostly on allochthonous sources of energy and nutrients, with strong dependence on the terrestrial ecosystem nearby (Faush et al. 2002; Soininen et al. 2015) and the loss or suppression of this element can alter the entire aquatic trophic web (Nakano et al. 1999). Terrestrial arthropods that fall in to stream channels represent a high-quality resource to fish (Mason and MacDonald 1982; Edwards and Huryn 1996; Wipfli 1997) and its input consists as paramount condition regulating the trophic cascade among insectivorous fish and peryphiton biomass (Nakano et al., 1999). In Serra da Bodoquena, channel and backwater drift feeders depends directly from the fallen resources from the tree canopy, mostly ants, contributing to the diet of 41% of the richness of the fish assemblage and the main resource to 14 species. Flowers, fruits and leaves were part of the diet of 23% of the fish fauna. In terms of fish frugivory, the most emblematic species of the region is the “piraputanga” *Brycon hilarii,* which is known from eating and dispersal several tree species (Reys et al. 2009), reinforcing the importance of large species in the seed dispersal syndrome (Galetti et al. 2008; Correa et al. 2015). However, small fish may present a yet poorly described role on this ecological process since fruits and seeds were found on *Astyanax* (*A. abramis*, *A. lacustris*, *A. lineatus* and *A. marionae*) guts on this work, and even the smaller *Hyphessobrycon luetkenii* and *Jupiaba acanthogaster*. Although these species lack in biomass, they represent a significant number of the fish assemblage, besides their small size able them to reach shallower environments near the margins and reach resources that may be unavailable to larger fish. This finding reinforces the role of small sized fishes on frugivory, especially in the Upper Paraguay basin, as demonstrated by recent studies (Yule et al. 2015; Silveira et al. 2019; Brito et al. 2021).

Niche overlap is the joint of resources used by two or more species (Colwell and Futuyma 1971). In another words, the region in niche space that combines two or more contiguous niches (Hutchinson 1958). Due space and resource limitations, trophic niche overlaps are common in nature, when different species can occupy a similar trophic niche and compete or share for similar resources (Pimm 2002). In this sense, nestedness webs minimizes competition and increases the number of coexisting species (Bastolla et al. 2009). Werner and Gilliam (1984) suggested that diet shifts occur when the niche of smaller size-classes is included in that of larger classes, resulting in a nested pattern. This pattern was also observed in Correa et al. (2016) to frugivorous fish in Neotropical wetlands, when large-bodied fish species is both a generalist and highly connected, serving key seed dispersal roles not achieved by smaller fish species. Allied to size differentiation, the vertical stratification of fishes can lead to a nestedness pattern, if we consider resources being allochthonous and autochthonous. Species inhabiting the water top will be able to feed on more allochthonous resources them that living on the bottom. This nested pattern also contributed to the high specialization in interactions. High intimacy between species can imply in high specialization (Pires and Guimarães 2013). In our system, high intimacy can be observed, for instance, between frugivorous fishes and fruits (e.g., *Brycon hilarii*). This species eats preferred preys in major degree in relation to the availability of the prey, increasing the specialization in the trophic web. Usually to fishes, feeding patterns are correlated with morphological differentiation (Casatti and Castro 2006), leading to some degree of specialization of unique morphotypes. According to Araujo et al. (2021), large frugivorous fish tend to be less specialized that small individuals, indicating a size dependent specialization to frugivorous fishes. This specialization is also related to water column, where fish with benthic habits will only have access to species of fruit that sink. While the occurrence of species in the water column allows access to a greater diversity of fruits, including those that float and those that sink.

All animal diets are influenced by available food resources and foraging strategies (Spitz et al. 2011). A high degree of modularity found is related to trophic guilds of fishes in communities. Species phylogenetically closely related tend to have more similar dietary preferences than unrelated species (Fontaine and Thébault, 2015). To reef fishes, phylogenetic conservatism is readily apparent at the family level, leading to groups strongly phylogenetically structured (Parravicini et al. 2020).

Invasive species are a major threat to the regime of aquatic communities (Havel et al. 2015). Main negative effects in small scale approaches the reduction of native species diversity, habitat alteration, hybridization, competition, predation and parasitism, and in major overview, changes in the structure of food webs, nutrient cycling and ecosystem function, consequently (Simberloff and Rejmánek 2011). Also, the presence of non-native species can be interpreted as an important proxy of habitat degradation in Neotropical streams, since the loss of ecologic integrity of habitats tend to exclude native species and the underexploited resources favour generalist non-native species, especially detritivores (Ruaro et al. 2018). In view of this, the presence of *Poecilia reticulata* in urban streams from Formoso drainage can be interpreted as a result of habitat degradation due the urban impacts. This small species feeds on fine particulate matter in suspension in the water and, as common in Poeciliinae, presents a superfetaceous reproduction strategy, which permits fast colonization of new habitats. Also, it can be considered a biodindicator of impacted sites (Ruaro et al. 2016). Its presence in Serra da Bodoquena streams and the significative food overlap between this species and another eight can be an alarming initial perspective about interference of *P. reticulata* over native food web. Moreover, in terms of species richness, Perdido river presents the lesser number of species but this drainage holds proportionally most of the endemism in Serra da Bodoquena. From the fifteen species found in this basin, two species are restricted ranged and four still undescribed. However, in this drainage also was found already an exotic species within the PNSB boundaries, *Coptodon rendalli*. Although its impact over the local native fauna still unclear, it is known that Pseudocrenilabrinae, *i.e.*, "tilápias" from *Coptodon* and *Oreochromis* genus, affect trophic webs through competition of resources, especially small particles as phytoplankton, zooplankton (Vicente and Fonseca-Alves 2013) and periphyton (Huchette et al. 2020). This unknown impact is reinforced by recent changes in aquaculture laws which facilitates the creation of alien species, such as tilápias, which entails in a consequent increase of the spread of this species on native locations (Dias et al. 2021) such as, in this case, a conservation unit of integral protection.

3.5 References

Albouy C, Archambault P, Appeltans W et al. (2019) The marine fish food web is globally connected. Nat Ecol Evolut 3:1153-1161

Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. Environ Model Softw 26:173-178

Araujo JM, Correa SB, Penha J, Anderson J, Traveset A (2021) Implications of overfishing of frugivorous fishes for cryptic function loss in a Neotropical floodplain. J Appl Ecol 58(7):1499-1510

Barabási A-L. (2016) Network science. Cambridge: Cambridge University Press

Bastolla U, Fortuna MA, Pascual-García A, Ferrera A, Luque B, Bascompte J (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018-1020

Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant–animal mutualistic networks. Proc Natl Acad Sci 100:9383-9387.

Beckett SJ (2016) Improved community detection in weighted bipartite networks. R Soc Open Sci 3(1):140536

Berg MB, Hellenthal RA (1992) The role of chironomidae in energy flow of a lotic ecosystem. Neth J Aquat Ecol 26:471-476

Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. BMC Ecol 6:9

Brito AK, Covich AP, Severo-Neto F, Gimênes-Jr H, Laps RR, Sabino J, Roque FO (2021) Diploendozoochory in Neotropical fish makes seed germination unlikely. Biotrop 53(5):1261-1264

Britski HA, Silimon KZS, Lopes BS (2007) Peixes do Pantanal. Manual de identificação. 2ed. Brasília, Embrapa

Burgos EB et al. (2007) Why nestedness in mutualistic networks? J Theor Biol 21:307-313

Campião KM, Ribas A, Tavares LER (2015) Diversity and patterns of interaction of an anuran–parasite network in a neotropical wetland. Parasitol 142:1751-1757

Casatti L, Castro RMC (2006) Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. Neotrop Ichthyol 4(2):203-214

Casey JM, Meyer CP, Morat F, Brandl SJ, Planes S, Parravicini V (2019) Reconstructing hyperdiverse food webs: gut content metabarcoding as a tool to disentangle trophic interactions on coral reefs. Methods Ecol Evol 10:1157-1170

Ceron K, Oliveira- Santos LGR, Souza CS, Mesquita DO, Caldas FL, Araujo AC, Santana DJ. (2019) Global patterns in anuran–prey networks: structure mediated by latitude. Oikos 128(11):1537-1548

Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52:567-576

Correa S, Araújo J, Penha J, Cunha C, Bobier K, Anderson J (2016) Stability and generalization in seed dispersal networks: a case study of frugivorous fish in Neotropical wetlands. Proc R Soc B 283:20161267

Correa SB, Araújo JK, Penha JM, Cunha CN, Stevenson PR, Anderson JT (2015) Overfishing disrupt an ancient mutualism between frugivorous fish and plants in Neotropical wetlands. Biol Conserv 191:159-167

Dala-Corte RB, Melo AS, Siqueira T, Bini LM, Martins RT, Cunico AM, Monteiro-Júnior CS et al (2020) Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region. J Appl Ecol 57(7):1391-1402

Dias RM, Pelicice FM, Tófoli RM, Alves GHZ, Lopes TM, Castello L, Tonella LH, Espínola LA, Agostinho AA (2021) Brazil’s leading environmental agency and aquatic biodiversity threatened by federal decree. An Acad Bras Cienc 93(4):e20200175

Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: analysing ecological networks. R News 8:8

Edwards ED, Huryn AD (1996) Effect of riparian land use on contributions of terrestrial invertebrates to streams. Hydrobiologia 337:151-159

Eero M, Dierking J, Humborg C, Undeman E, MacKenzie BR, Ojaveer H, Salo T, Köster FW (2021) Use of food web knowledge in environmental conservation and management of living resources in the Baltic Sea, ICES J Mar Sci fsab145

Escarpinati SC, Siqueira T, Medina Jr P, Roque FO (2014) Short-term effects of visitor trampling on macroinvertebrates in karst streams in an ecotourism region. Environ Monit Assess 186(3):1655-1663

Fausch KD, Torgersen CE, Baxter CV, Li HW (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483-498

Fontaine C, Thébault E (2015) Comparing the conservatism of ecological interactions in plant-pollinator and plant-herbivore networks. Pop Ecol 57:29-36

Freitas TMS, Montag LF, Barthem RB (2017) Distribution, feeding and ecomorphology of four species of Auchenipteridae (Teleostei: Siluriformes) in Eastern Amazonia, Brazil. Iheringia Ser Zool 107:e2017008.

Galetti M, Donatti CI, Pizo MA, Giacomini H (2008) Big fish are the best: seed dispersal of *Bactris glaucescens* by the pacu fish (*Piaractus mesopotamicus*) in the Pantanal, Brazil. Biotropica 40:386-389

Havel JE, Kovalenko KE, Thomaz SM, Amalfitano S, Kats LB (2015) Aquatic invasive species: challenges for the future. Hydrobiol 750:147-170

Horn HS (1966) Measurement of “overlap” in comparative ecological studies. Am Nat 100:419-424.

Huchette SMH, Beveridge MCM, Baird DJ, Ireland M (2000) The impacts of grazing by tilapias (*Oreochromis niloticus* L.) on periphyton communities growing on artificial substrate in cages. Aquac 186:45-60

Hutchinson GE (1958) Concluding remarks. Cold Spring Harbor Symp Quant Biol 22:415-427

Hynes HBN (1950) The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J Anim Ecol 19(1):36

ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade) (2013) Plano de manejo do Parque Nacional da Serra da Bodoquena. Encarte 3 – Análise do PNSB.

Available at www.icmbio.gov.br/portal/images/stories/docs-planos-de-manejo/Encarte3_serra_da_bodoquena.pdf

Janjua MY, Gerdeaux D (2011) Evaluation of food web and fish dietary niches in oligotrophic Lake Annecy by gut content and stable isotope analysis. Lake Reserv Manag 27:115-127

Krebs CJ (1998) Ecological methodology. New York, Benjamin/Cummings Publishers

Liu X, Murata T (2010) Advanced modularity-specialized label propagation algorithm for detecting communities in networks. Phys Stat Mech Its Appl 389(7):1493-1500

Mason CF, MacDonald SM (1982) The input of terrestrial invertebrates from tree canopies to a stream. Freshw Biol 12:305-311

Nakano S, Miyasaka H, Kuhara N (1999) Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435-2441

Navarro J, Grémillet D, Ramirez FJ, Afán I, Bouten W, Forero MG (2017) Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes. Mar Ecol Progr Ser 578:243-51

Necchi Jr. O, Branco LHZ (1992) Preliminary evaluation of primary production in a stream of São Paulo State, Southeastern Brazil. Rev Bras Biol 52:319-324

Olesen JM, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. Proc Natl Acad Sci 104:19891-19896

Oliveira MD, Calijuri MC (1996) Estimate of the rate of primary production in two lotic systems, based on hourly change of dissolved oxygen – Itaqueri and Lobo Rivers (São Paulo State). An Acad Bras Cienc 68:103-111

Parravicini V, Casey JM, Schiettekatte NMD, Brandl SJ, Pozas-Schacre C, Carlot J, Edgar GJ, Graham NAJ, Harmelin-Vivien M, Kulbicki M, et al (2020) Delineating reef fish trophic guilds with global gut content data synthesis and phylogeny. PLOS Biol 18(12):e3000702

Patefield WM (1981) Algorithm AS 159: an efficient method of generating random R×C tables with given row and column totals. J R Stat Soc Ser C Appl Stat 30:91-97

Pereira RAC, Resende EK (1998) Peixes detritívoros da planície inundável do rio Miranda, Pantanal, Mato Grosso do Sul, Brasil. EMBRAPA/CPAP 12:50

Pimm SL (2002) Food webs, Chicago, IL: University of Chicago Press

Pires MM, Guimarães Jr PR (2013) Interaction intimacy organizes networks of antagonistic interactions in different ways. J R Soc Interface 10:20120649

Power ME, Dietrich WE (2002) Food webs in river networks. Ecol Res 17:451-471

R Core Team. R: A language and environment for statistical computing. (2020) Vienna, Austria: R Foundation for Statistical Computing

Reys P, Sabino J, Galetti M (2009) Frugivory by the fish *Brycon hilarii* (Characidae) in western Brazil. Acta Oecol 35:136-141

Richard K, Wallace JR (1981) An assessment of diet-overlap indexes. Trans Am Fish Soc 110:72-76

Roughgarden J (1972) Evolution of niche width. Am Nat 106(952):683-718

Ruaro R, Gubiani ÉA, Cunico AM et al (2016) Comparison of fish and macroinvertebrates as bioindicators of Neotropical streams. Environ Monit Assess 188:45

Ruaro R, Mormul RP, Gubiani ÉA, Piana PA, Cunico AM, da Graça WJ (2018) Non-native fish species are related to the loss of ecological integrity in Neotropical streams: a multimetric approach. Hydrobiol 817:413-430

Saunders WC, Bouwes N, McHugh P, Jordan CE (2018) A network model for primary production highlights linkages between salmonid populations and autochthonous resources Ecosphere 9:3

Severo-Neto F, Teresa FB, Froehlich, O (2015) Ecomorphology and diet reflect the spatial segregation between two Siluriformes species inhabiting a stream of the Bodoquena Plateau, in Central Brazil. Iheringia, Série Zoologia 105(1):62-68.

da Silva JC, Gubiani ÉA, Neves MP, Delariva R (2017) Coexisting small fish species in lotic neotropical environments: evidence of trophic niche differentiation. Aquat Ecol 51:275-288

Silveira R, Leão-Neto WM, Barbosa FH (2019) Small-sized fish as possible seed dispersers: disclosing novel fish and plant species interactions in the Pantanal wetland. Stud Neotrop Fauna Environ 55(1):36-43

Simberloff D, Rejmánek M (2011) Encyclopedia of biological invasions. University of California Press, California

Soininen J, Bartels P, Heino J, Luoto M, Hillebrand H (2015) Toward more integrated ecosystem research in aquatic and terrestrial environments. Bioscience 65:174-182

Spitz J, Cherel Y, Bertin S, Kiszka J, Dewez A, et al (2011) Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. Deep Sea Res. I.

Teng J, McCann KS (2004) Dynamics of compartmented and reticulate food webs in relation to energetic flows. Am Nat 164:85-100

Valdovinos FS (2019) Mutualistic networks: moving closer to a predictive theory. Ecol Lett 22:1517-1534

Vander Zanden MJ Vadeboncoeur Y (2002) Fishes as integrators of benthic and pelagic food chains in lakes. Ecology 83:2152-2161

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137

Velasquez GG, Spanhol CP, Pedroso EA, Araújo EG (2014) Stakeholders, Ecotourism and Sustainable Development: The Case of Bonito, Mato Grosso Do Sul State, Brasil. Int J Cult Tour Hosp Res 2(1):133-153

Vicente IST, Fonseca-Alves CE (2013) Impact of introduced Nile tilapia (*Oreochromis niloticus*) on non-native aquatic ecosystems. Pak J Biol Sci 16(3):121-126

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Evol Syst 15:393-425

Winemiller KO, Agostinho AA, Caramaschi EP (2008) Fish ecology in tropical streams. In: Dudgeon D (ed) Tropical stream ecology. Elsevier/Academic Press, San Diego, pp 107-146

Winemiller KO, Jepsen DB (1998) Effects of sazonality and fish movement on tropical river food webs. J Fish Biol 53(A):267-296

Wipfli MS (1997) Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Can J Fish Aquat Sci 54:1259-1269

Xia Y, Li Y, Zhu S, Li J, Li S, Li X (2020) Individual dietary specialization reduces intraspecific competition, rather than feeding activity, in black amur bream (*Megalobrama terminalis*). Scientific Rep 10(1):17961

Yule TS, Severo-Neto F, Tinti-Pereira AP, Corrêa da Costa LBL (2015) Freshwater sardines of the pantanal delay seed germination in a floodplain tree species. Wetlands 36:195-199

Zanata TB, Dalsgaard B, Passos FC, Cotton PA, Roper JJ, Maruyama PK, Fischer E, Schleuning M, Martín González AM, Vizentin- Bugoni J (2017) Global patterns of interaction specialization in bird–flower networks. J Biogeogr 44(8):1891-1910

Zhang J (2016) Package “spaa”. Miscellaneous functions for analysing species association and niche overlap

3.6 Supplementary material

Table 1. Fish species registered in the Serra da Bodoquena streams, respective code and and the contribution of feeding items in the diet of the community.

Taxa	Code								
CHARACIFORMES		Fish	Scales	Autochthonous invertebrates	Allochthonous invertebrates	Algae	Periphyton	Plant	Detritus
Parodontidae									
Parodon nasus Kner, 1859	Parnas	0	0	0	0	0.25	0.75	0	0
Curimatidae									
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)	Stebre	0	0	0	0	0	0	0	1
Steindachnerina nigrotaenia (Boulenger, 1902)	Stenig	0	0	0	0	0	0	0	1
Prochilodontidae									
Prochilodus lineatus Valenciennes, 1836	Prolin	0	0	0	0	0	0	0	1
Anostomidae									
Leporinus friderici Bloch, 1794	Lepfri	0	0	0	0.1	0	0	0.9	0
Leporinus striatus Kner, 1858	Lepstr	0	0	0.9	0.05	0	0	0.05	0
Crenuchidae									
Characidium borellii (Boulenger, 1895)	chabor	0	0	0.98	0.02	0	0	0	0
Characidium aff. *zebra* Eigenmann, 1909	chazeb	0	0	0.9	0.1	0	0	0	0
Gasteropelecidae									
Thoracocharax stellatus (Kner, 1858)	thoste	0	0	0	1	0	0	0	0

Characidae									
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	aphani	0	0.18	0.62	0.2	0	0	0	0
Aphyocharax dentatus Eigenmann and Kennedy, 1903	aphden	0.16	0	0.25	0.59	0	0	0	0
Astyanax abramis (Jenyns, 1842)	astabr	0	0.05	0.12	0.66	0	0	0.17	0
Astyanax lacustris (Lütken, 1875)	astlac	0	0.01	0.11	0.49	0	0	0.39	0
Astyanax lineatus (Perugia, 1891)	astlin	0	0.01	0.48	0.26	0	0	0.25	0
Astyanax marionae Eigenmann, 1911	astmar	0	0	0.14	0.74	0	0	0.12	0
Astyanax sp. 1	astspu	0	0	0,44	0,36	0	0	0,2	0
Astyanax sp. 2	astspd	0	0	0,03	0,97	0	0	0	0
Brachychalcinus retrospina Boulenger, 1892	braret	0	0	0,13	0,79	0	0	0,08	0
Brycon hilarii (Valenciennes, 1850)	bryhil	0	0	0	0.11	0	0	0.89	0
Bryconamericus exodon Eigenmann, 1908	bryexo	0	0	0.95	0.05	0	0	0	0
Bryconops melanurus (Bloch, 1794)	brymel	0	0	0.05	0.88	0	0	0.07	0
Creagrutus meridionalis Vari & Harold, 2001	cremer	0	0	0.75	0.01	0	0	0.24	0
Deuterodon luetkenii (Boulenger, 1887)	hemlun	0	0	0.18	0.7	0	0	0.12	0
Hemigrammus lunatus Durbin, 1918	hypequ	0	0	1	0	0	0	0	0
Hyphessobrycon eques Steindachner, 1882	hyplue	0	0	0.52	0.3	0	0	0.18	0
Jupiaba acanthogaster (Eigenmann, 1911)	jupaca	0	0.09	0.58	0.2	0.13	0	0	0
Moenkhausia bonita Benine, Castro & Sabino, 2004	moebon	0	0	0.2	0.8	0	0	0	0

Moenkhausia oligolepis (Günther, 1864)	moeoli	0	0	0.05	0.95	0	0	0	0
Odontostilbe pequira (Steindachner, 1882)	odopeq	0	0	0.1	0.01	0.88	0	0.01	0
Oligosarcus perdido Ribeiro, Cavallaro & Froehlich, 2007	oliper	1	0	0	0	0	0	0	0
Phenacogaster tegatus (Eigenmann, 1911)	pheteg	0	0	0.33	0.67	0	0	0	0
Piabarchus analis (Eigenmann, 1914)	piaana	0	0	0.08	0.9	0	0	0.02	0
Piabarchus torrenticola Mahnert & Géry, 1988	piator	0	0.12	0.63	0.25	0	0	0	0
Poptella paraguayensis (Eigenmann, 1907)	poppar	0	0	0	1	0	0	0	0
Psellogrammus kennedyi Eigenmann, 1903	pseken	0	0	0.7	0.3	0	0	0	0
Salminus brasiliensis (Cuvier, 1816)	salbra	1	0	0	0	0	0	0	0
Serrapinnus calliurus (Boulenger, 1900)	sercal	0	0	0.01	0	0.99	0	0	0
Serrasalmus marginatus Valenciennes, 1837	sermar	0.8	0.2	0	0	0	0	0	0
Xenurobrycon macropus Myers & Miranda Ribeiro, 1945	xenmac	0	0	0.63	0.37	0	0	0	0
Acestrorhynchidae									
Acestrorhynchus pantaneiro Menezes, 1992	acepan	1	0	0	0	0	0	0	0
Erythrinidae									
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	hopuni	0.1	0	0.9	0	0	0	0	0
Hoplias malabaricus (Bloch, 1794)	hopmal	0.5	0	0	0.5	0	0	0	0
Lebiasinidae									

Pyrrhulina australis Eigenmann & Kennedy, 1903	Pyraus	0	0	0.4	0.53	0	0	0.07	0
SILURIFORMES									
Aspredinidae									
Bunocephalus doriae Boulenger, 1902	bundor	0	0	0.6	0	0	0	0	0.4
Trichomycteridae									
Ituglanis herberti (Miranda Ribeiro, 1940)	ituher	0	0	1	0	0	0	0	0
Callicththyidae									
Callichthys callichthys (Linneaus, 1758)	calcal	0	0	0.7	0	0	0	0	0.3
Corydoras aeneus (Gill, 1858)	coraen	0	0	0.68	0.04	0	0	0	0.28
Loricariidae									
Ancistrus sp.	ancsp	0	0	0	0	0	1	0	0
Farlowella paraguayensis Retzer and Page, 1997	farpar	0	0	0	0	0	0	0	1
Hemiodontichthys acipenserinus (Kner, 1853)	hemaci	0	0	0.3	0	0	0.3	0	0.4
Hypostomus basilisko Tencatt, Zawadzki & Froehlich, 2014	hypbas	0	0	0	0	0	0.75	0	0.25
Hypostomus froehlichi Zawadzki, Nardi & Tencatt, 2021	hypfro	0	0	0	0	0	0.4	0	0.6
Hypostomus perdido Zawadzki, Tencatt & Froehlich, 2014	hypper	0	0	0	0	0	0.3	0	0.7
Hypostomus sp. 2	hypespd	0	0	0	0	0	0.5	0	0.5
Loricaria luciae Thomas, Rodriguez, Cavallaro, Froehlich & Castro, 2013	lorluc	0	0	0.3	0	0	0.7	0	0
Otocinclus vittatus Regan, 1904	otovit	0	0	0	0	0	0.5	0	0.5
Rineloricaria lanceolata (Günther, 1868)	rinlan	0	0	0	0	0	1	0	0

Rineloricaria parva (Boulenger, 1895)	rinpar	0	0	0	0.01	0	0.5	0	0.49
Pseudopimelodidae									
Pseudopimelodus mangurus (Valenciennes, 1835)	pseman	0,85	0	0,15	0	0	0	0	0
Heptapteridae									
Imparfinis schubarti (Gomes, 1956)	impsch	0	0	1	0	0	0	0	0
Phenacorhamdia sp.	phesp	0	0	0.8	0.2	0	0	0	0
Pimelodella taenioptera Ribeiro, 1914	pimtae	0	0.07	0.8	0.03	0	0	0.1	0
Rhamdia quelen (Quoy & Gaimard, 1824)	rhaque	0.04	0.01	0.39	0.29	0	0	0.27	0
Pimelodidae									
Pseudoplatystoma reticulatum Eigenmann & Eigenmann, 1889	pseret	1	0	0	0	0	0	0	0
Auchenipteridae									
Tatia neivai (Ihering, 1930)	tatnei	0	0	0.5	0.5	0	0	0	0
GYMNOTIFORMES									
Gymnotidae									
Gymnotus carapo Linnaeus, 1758	gymcar	0	0	0.67	0.33	0	0	0	0
Sternopygidae									
Sternopygus macrurus (Bloch and Schneider, 1801)	stermac	0	0	1	0	0	0	0	0
Apteronotidae									
Apteronotus caudimaculosus de Santana, 2003	aptcau	0	0	1	0	0	0	0	0
CYPRINODONTIFORMES									
Poeciliidae									
Poecilia reticulata Peters, 1859	poeret	0	0	0.1	0.2	0	0	0	0.7
BELONIFORMES									

Belonidae									
Potamorrhaphis eigenmanni Ribeiro, 1915	poteig	0.8	0	0	0.2	0	0	0	0
SYNBRANCHIFORMES									
Synbranchidae									
Synbranchus marmoratus Bloch, 1795	synmar	0.33	0	0.67	0	0	0	0	0
CICHLIFORMES									
Cichlidae									
Aequidens plagiozonatus Kullander, 1984	aeqpla	0	0.02	0.73	0	0	0	0.1	0.15
Australoheros sp.	aussp	0	0	0.2	0.1	0.2	0	0.5	0
Bujurquina vittata (Heckel, 1840)	bujvit	0	0	0.75	0	0	0	0	0.25
Cichlasoma dimerus (Heckel, 1840)	cicdim	0	0	0.2	0.1	0.1	0	0.35	0.25
Coptodon rendalli (Boulenger, 1897)	copren	0	0	0.2	0	0.2	0	0	0.6
Crenicichla lepidota Heckel, 1840	crelep	0	0	0.97	0.03	0	0	0	0
Crenicichla vittata Heckel, 1840	crevit	0.75	0	0.25	0	0	0	0	0

Table 2. Code and referent resources of items consumed by fish fauna from Serra da Bodoquena streams.

CODE	RESOURCE
A	Fish
B	Scales
C	Coleoptera
D	Diptera
E	Chironomidae
F	Ephemeroptera
G	Odonata
H	Trichoptera
I	Plecoptera
J	Hemiptera
K	Lepidoptera
L	Megaloptera
M	Aquatic fragments
N	Gastropoda
O	Cladocera
P	Ostracoda
Q	Copepoda
R	Nematoda
S	Algae
T	Periphyton
U	Tecameba
V	Frutis
X	Flowers
Z	Leaves
AA	Seeds
AB	Aranae
AC	Acari
AD	Coleoptera
AE	Lepidoptera
AF	Ephemeroptera
AG	Hymenoptera
AH	Formicidae
AI	Diptera
AJ	Ensifera
AK	Isoptera
AL	Hemiptera
AM	Thysanoptera
NA	Neuroptera
AO	Orthoptera
AP	Plecoptera
AQ	Diplopoda
AR	Terrestrial fragments
AS	Detritus

Chapter 3

(formatting rules follow Hydrobiologia journal)

4 Fish taxonomic and functional diversity across elevation and deforestation gradients in karst streams from Midwest Brazil

4.1 Introduction

One of the major goals in community ecology studies is the comprehension of how communities organize through seasonal/temporal and spatial scales (Cavender-Bares et al., 2009). For fish assemblages, seasonal/temporal scales help elucidate circadian behaviors shifting (Helfman, 1981), predator-prey relationships (Trenkel et al., 2005), occupation of seasonally flooded environments (Davis, 1988; Ortega et al., 2015) and the response to anthropogenic disturbances (Beukhof et al., 2019; Zeni et al., 2020). From a spatial perspective, fish assemblages may be structured as a result of spatial patterns (Carvalho & Tejerina-Garro, 2014), such as natural (e.g., longitudinal, elevation) and anthropogenic (e.g., deforestation, urbanization) environmental gradients. In a finer scale, species distribution can be subject to habitat constraints, which can favor or limit organisms' occurrence and abundance in a specific site. These constraints are the theoretical basis of the environmental filtering concept (Smith & Powell, 1971). According to this model, the establishment of a species in a given locality depends on its capacity to pass through the successive environmental filters from a large (regional) to a fine (local) scale. Most of this selection is based on the species phenotypical traits, especially morphology (Poff, 1997). As a consequence, local fish assemblages tend to share similar traits matching these environmental filters (Mouillot et al., 2007). However, niche-based processes, such as species interactions can limit the occurrence of species with similar traits as proposed by MacArthur & Levins (1967) in the limiting similarity hypothesis which, in essence, predicts that species that share similar traits are not expected to coexist.

In this context, spatial and temporal patterns of species compositon, changes can be driven not only by niche and dispersal-based processes, but also through selective colonization/extinction or habitat filtering (Baselga, 2010). The species composition dissimilarity between localities of a given area is known as the beta diversity, which can be partitioned in the turnover and nestedness components (Heino et al., 2015). Turnover represents the replacement of species among sites and can result from niche and dispersal processes, whereas nestedness represents a non-random gain or loss of species among sites due to selective colonization/extirpation or habitat nestednes (Baselga, 2010; Socolar et al., 2016; Zeni et al., 2020).

In streams, fish community ecology aims to investigate how species change along the stream continuum, namely, the longitudinal gradient (Roberts & Hitt, 2010). Stream habitats are heterogeneous systems composed by a multi-scaled mosaic of patches on a mesohabitat scale, such as pools, riffles and runs (Frissell et al., 1986) delimited by different combinations of current, depth, and substrate composition (Angermeier & Schlosser, 1989) that change along the longitudinal gradient (Vannote et al, 1980). The longitudinal habitat structure in streams directly influences on structure and composition of ichthyofauna (Schwartz & Herricks, 2008) with the increase of species richness in a downstream direction (Winemiller et al., 2008). Longitudinal nestedness implies the action of a persistent environmental constraint (e.g., decreased habitat availability, increased disturbance intensity) that has “filtered” species out of upstream communities (Poff, 1997).

The main human activity associated to changes to local and regional species composition and global biodiversity loss is the conversion of natural ecosystems into agricultural systems (Tscharntke et al., 2005; Dolédec & Statzner, 2010). The simplification of highly complex ecosystems in homogeneous landscapes jeopardize the occurrence of sensitive species while facilitates the colonization and establishment of less demanding ones in an unstable environment (Scott & Helfman, 2001; Brejão et al., 2018). Along with the impacts over the local species composition, the landscape homogeneity common to agroecosystems, since large areas are converted to the same crop (i.e., monoculture), tends to artificially select functionally similar species across multiple sites (Ekroos et al., 2010) contributing to a biological homogenization (*i.e.*, decrease in beta diversity) (Karp et al., 2012; Segre et al., 2014). From a point of view more concearning, studies that approach these impacts over β-diversity and its facets (*i.e.,* taxonomic, functional and phylogenetic) still recents (e.g., Casatti et al., 2015, Roa-Fuentes et al., 2019, Zeni et al., 2020), agricultural practices are secular and almost 40% of the planet surface is already occupied by agroecosystems (Ramankutty et al. 2008). Merely in Brazilian Cerrado biome, the crop area increased by 80% between 1996 to 2006 (Merten et al., 2010). Moreover, along with the biodiversity loss and hogenization, large scale agricultural activities affect water quality (Bareswill et al., 2013), promoves erosion increase (Merten & Minella, 2013) and are responsible by changes in hydrological regime of watersheds (Chaves et al., 2007; Costa et al., 2003). In this sense, urgent efforts are needed in order to a profound comprehensal of how land use affect the distribution of the organisms, especially in the megadiverse Neotropical region.

Neotropical streams figure as one of the world´s biodiversity hotspots (Dudgeon, 2019). In this scenario, almost 3500 species are found in Brazilian streams (Castro, 2021) and many of them present a restricted distribution and/or are threatened due anthropic disturbs (Reis et al., 2016). One of the most understudied Brazilian basin in terms of stream-dwelling fishes is the Upper Paraguay River basin (UPRB). This basin is part of the La Plata South American drainage and its main water course is the Paraguay River. The lowlands where Paraguay River runs, known as Pantanal, are subject to seasonal flood pulses that floods the plains nearby and worldwide recognized for its biodiversity. Although most of Pantanal hydrological system is based on this flooding dynamic of large rivers, headwaters ecosystems are small streams located in the highlands that surround the basin. In the Southwestern portion of Pantanal area is found the Serra da Bodoquena. This karst system represents an important source of economic income to Mato Grosso do Sul state, due the tourism and agricultural activities. The occupation of the region goes back to the 1960's, when the first areas were colonized to livestocking. However, recent changes in the economic activity switched those areas in agricultural landscapes, especially for soybean and corn production. While the effects of this recent land use change can already be seen in the decreasing of the cristallinity of the rivers during the rainy season, impacts over the fish fauna composition still uncertain. Thus, this chapter aims to determine whether the taxonomic and functional compositions of fish assemblages are affected along the natural (altitude) and (deforestation) gradients affects in Serra da Bodoquena streams.

4.2 Methods

Study area

The Serra da Bodoquena is situated in the southwest of Mato Grosso do Sul state, in the Central-Western region of Brazil (Figure 1). With a karst formation and whose origin dates back to the Precambrian (Sallun Filho & Karmann, 2007), this region still preserves much of its original vegetation cover intact, especially in the higher areas, where the headwaters streams that drain into rivers of the Upper Paraguay River basin are located (ICMBIO, 2013). In the Western border of Serra da Bodoquena is found the Parque Nacional da Serra da Bodoquena (PNSB). Created in 2000, the park is the single federal conservation unit of integral protection in the Mato Grosso do Sul state. It covers an area of 76,000 hectares, divided in North and South portions that have two main drainages: in the North portion, the Salobra river and Perdido river, in the South. Although headwaters of both rivers are outside the PNSB boundaries, their major extension are within the park limits. Regarding the flow direction, the Salobra river flows towards North, in direction of Miranda River, its main river watershed; while the Perdido river flows towards South, in direction of Apa river, its main watershed and the South limit of Upper Paraguay River basin. Beyond these two main rivers, the park South portion also harbors the headwaters of Formoso and Prata rivers, both from Miranda basin. In contrast to the rivers inserted within the PSNB, these latter ones occur in a smoother terrain, being more exposed to anthropogenic impacts of economic activities, such as livestock, road crossing, agriculture and tourism. Native forests surrounding the park are fragmented by cattle ranching and soybeans and corn monocultures, resulting in a mosaic of land cover that ranges from dense native vegetation to agroecosystems of pasture and agriculture. In terms of slope, Formoso basin reaches from 484 to 220 m.a.sl. within the 5km between headwaters to the outfall in Miranda River while Salobra River goes from 622 to 125 in the 10 km straight between the headwaters and Miranda River.

Fish sampling

Fish assemblages were sampled between 2003 to 2018 in 33 streams from first to third order in Serra da Bodoquena region, from which, 10 corresponded to Salobra River basin and 23 to Formoso River basin. Samplings occurred in stretches from 100 to 200 meters length and Vouchers specimens are deposited in the Coleção Zoológica da Universidade Federal de Mato Grosso do Sul (ZUFMS). Identification of fish species follows Britski et al. (2007) and original descriptions.

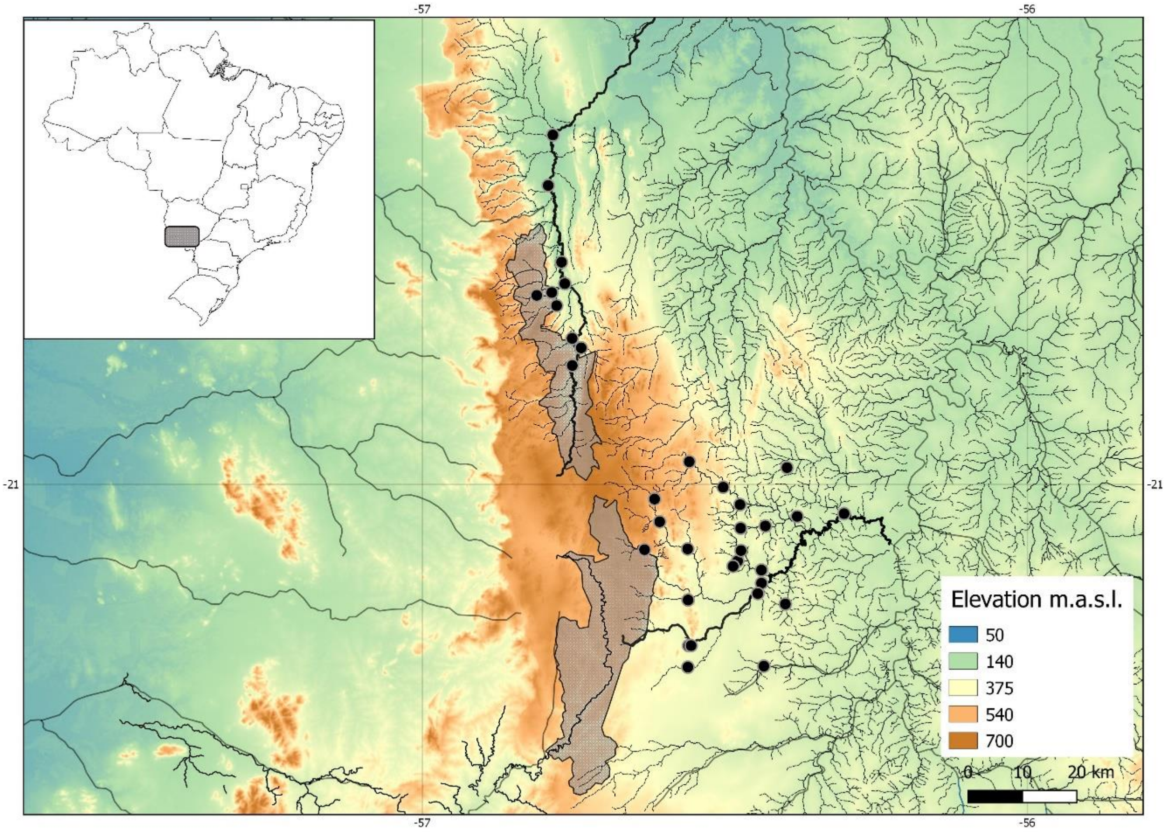

Figure 1 – Location of Serra da Bodoquena in Southwestern Brazil and the studied drainages. Above, Salobra River drainage and Formoso River drainage below. Black dots represent fish samples sites. Source: Prepared by the author.

Functional traits

To access the functional traits of each species, 15 ecomorphological attributes related to food intake, habitat preferences and locomotion were chosen based on Leitão et al. (2016) (Table 1). The set of traits was based on 17 morphological measures: body depth (BD), body width (BW), mouth width (MW), mouth depth (MD), snout length (SN), protrusion length (PRT), caudal-peduncle minimal depth (CPD), caudal-fin depth (CFD), caudal-fin surface (CFS), distance between the insertion of pectoral fin to the bottom of the body (PFI), body depth at the level of the pectoral-fin insertion (PFB), pectoral-fin length (PFL), pectoral-fin surface (PFS), head depth along the vertical axis of the eye (HD), eye diameter (ED), distance between the center of the eye to the bottom of the head (EH), distance from the top of the mouth to the bottom of the head along the head depth axis (MO); and mass. Specimens were weighted using an electronic balance (0.001 g) and linear measures were taken with a digital caliper. Surface measures were calculated in ImageJ software, through digital pictures of the drawing of the fins on graph paper. Species that do not have pectoral or caudal fins, the value of the functional trait related to the absent fin was fixed to 0.

Table 1. Functional attributes based on Leitão et al. (2016), their calculation and ecological meaning used to assess fish functional diversity from Serra da Bodoquena streams, in Western Brazil.

Functional attributes	**Calculation**	**Ecological meaning**
Mouth-protrusion length (Prt)	Prt/Sn	Nature of food items captured and feeding method (Leitão et al., 2016)
Oral-gape surface (Osf)	$\frac{Mw \times Md}{Bw \times Bd}$	Nature/Size of food items captured (Leitão et al., 2016)
Oral-gape shape (Osh)	Md/Mw	Method to capture food items (Karpouzi & Stergiou 2003)
Oral-gape position (Ops)	Mo/Hd	Feeding method in the water column (Leitão et al., 2016)
Eye size (Edst)	Ed/Hd	Prey detection (Leitão et al., 2018)
Eye position (Eps)	Eh/Hd	Vertical position in the water column (Gatz, 1979)
Body transversal shape (Bsh)	Bd/B	Vertical position in the water column and hydrodynamism (Sibbing, Nagelkerke, 2001)
Body transversal surface (Bsf)	$\frac{\ln [\pi/4 \times Bw \times Bd + 1]}{\ln (Mass + 1)}$	Mass distribution along the body for hydrodynamism (Villéger et al., 2010)
Pectoral-fin position (PFps)	PFi/PFb	Pectoral fin use for maneuverability (Dumay et al., 2004)
Aspect ratio of the pectoral fin (PFar)	PFl^2/PFs	Pectoral fin use for propulsion (Leitão et al., 2016)
Caudal-peduncle throttling (CPt)	CFd/CPd	Caudal propulsion efficiency through reduction of drag (Webb, 1984)
Aspect ratio of the caudal fin (CFar)	CFd^2/CFs	Caudal fin use for propulsion and/or direction (Webb, 1984)
Fins surface ratio (Frt)	$2 \times PFs/CFs$	Main type of propulsion between caudal and pectoral fins (Villéger et al., 2010)
Fins surface to body size ratio (Fsf)	$\frac{(2 \times PFs) + CFs}{\pi/4 \times Bw \times Bd}$	Acceleration and/or maneuverability efficiency (Villéger et al., 2010)
Body mass (logM)	$\log (Mass + 1)$	Metabolism, endurance and swimming ability (Villéger et al., 2010)

Elevation and deforestation gradients

Initially, we built a buffer with 100 meters orthogonally to the water bodies. After that, we used the Land Use and Land Cover (LULC) Classification of the MapBiomas Project (Collection 3.0 of the Annual Series of Land Use and Coverage Maps of Brazil, accessed on 3/9/2020), with a resolution of 30 meters, to quantify our land use classes in the date of each the 33 sampling sites. Because the MapBiomas Project classification results in 11 classes for our study area, we have dissolved the classes into natural formation (*i.e.*, native forest, non-forest, wetland vegetation) and anthropogenic use (*i.e.*, agriculture, livestock and urban areas), using for this the QGIS software (version 3.4.13-Madeira). Finally, the areas for the two final classes were calculated. Data about altitude in meters above sea level (m.a.s.l.) of each collection point was obtained through a digital elevation model (DEM), generated in the QGIS software (version 3.4.13-Madeira). To verify whether the community of each drainage was influenced by the altitudinal or deforestation gradient, we used the presence/absence data of each site expressed in composed graph (Landeiro et al., 2013) ranked by each gradient. The relations were tested by a Multivariate Analysis of Variance with a Jaccard statistics on R environment.

Taxonomic and functional beta diversity

We partitioned global beta diversity (β_{SOR}) into turnover (β_{SIM}) and nestedness (β_{SNE}) components. The spatial beta diversity and its components were obtained using Sorensen dissimilarity index based on taxonomic and functional aspects of the assemblages. For taxonomic beta diversity, species composition (presence/absence data) was used. For functional beta diversity, a Principal Coordinate Analysis (PCoA) was used with the fifteen functional traits that were used as the functional composition for each stream reach. Both taxonomic and functional beta diversity were obtained for Formoso and Salobra separately because species composition between these two basins were different (Supplementary Material – Table 1).

Considering our aim and the analyses, mean values of beta diversity (β_{SOR}) and its components (β_{SIM} and β_{SNE}) were generated for each stream from the triangular matrices. To get these metrics, all the values of beta diversity, turnover and nestedness between a specific stream and all the other streams were summed and divided by the number of streams. The mean values of β_{SOR} ($\bar{x}\beta_{SOR}$) indicates how unique is the species and traits composition of one specific stream compared to the others, while mean values of β_{SIM} ($\bar{x}\beta_{SIM}$) and β_{SNE} ($\bar{x}\beta_{SNE}$) indicates how much of this uniqueness is due to replacement or loss/gain of species and functional traits. Values of $\bar{x}\beta_{SOR}$ close to 1 indicates sites more unique, while higher values of $\bar{x}\beta_{SIM}$ and $\bar{x}\beta_{SNE}$ indicates that the uniqueness is due to turnover and nestedness, respectively.

To test the influence of altitude and deforestation gradients in the mean beta diversity and its components for each basin, a Generalized Additive Model (GAM) was run. This model can identify non-linear relationships between response and predictors variables (Zuur et al., 2009). Since we identified an interaction between the basin and the predictors (altitude and deforestation gradients), we fitted models that contain different smoothers for each predictor variable in each basin. Models like this are generated using the “by” command and have been referred to as Varying-Coefficient Models (VCM, Hastie & Tibshirani, 1993). The inclusion of a factor with the “by” command sets up a model matrix that can use a separate smoother for each level of the factor (basin with 2 levels [Formoso and Salobra] in this case) and allows the interactions between smoothers and factors (Wood, 2021). Prior to this, we standardized our predictors and run a Pearson correlation aiming to identify highly correlated variables. As a result, the “native” land use was removed from the models because it was negatively correlated with “non-native” ($r>0.95$). We used “betapart” package (function:

beta.pair) for beta diversity partitioning, “vegan” for standardizing our variables (function: decostand) and for Pearson correlation (function: cor), and “mgcv” (function: gam) for GAM’s models. All the analyses were done on R environment, version 4.03.

4.3 Results

Formoso basin was the richest region, with 59 species, whilst Salobra held 51 species. Characiformes represented the richest order in both basins, with 36 and 25 species, respectively. Siluriformes was the second order with mores species, with 15 and 18. Twenty-one species were exclusive to Formoso and 13 in Salobra River basin. Cyprinodontiformes order was exclusive from Formoso, represented by the non-native species *Poecilia reticulata* and Beloniformes (*Potamorraphis eigenmanni*) was present only in Salobra streams.

Elevation and deforestation effects

Altitude of the sampling sites ranged from 236 to 502 m.a.s.l. in Formoso drainage and from 120 to 320 in Salobra drainage. A significant effect of altitude was found in the Salobra watershed (R^2 0.62, P=0.02; Figure 2) but no ordination of the species occurred in the Formoso watershed ($R^2$0.01, p=0.8; Figure 2). Species that contributed most to composition in higher strata of Salobra River was *Rhamdia quelen*, *Characidium zebra*, *Astyanax lineatus* and *Ancistrus* sp, while lower quotes were represented by *Brycon hilarii*, *Brachychalcinus retrospina*, *Otocinclus vittatus*, *Bunocephalus doriae*, *Hemiodontichthys acipensericus*, *Ituglanis herberti*, *Piabarchus analis* and *Serrapinnus calliurus*.

Native vegetation cover in Formoso basin ranged between 1.5 to 95% and 36 to 85% in Salobra basin. Despite the wide range of variation in both basins, no significative effects were found in the taxonomic neither functional composition along the deforestation gradient.

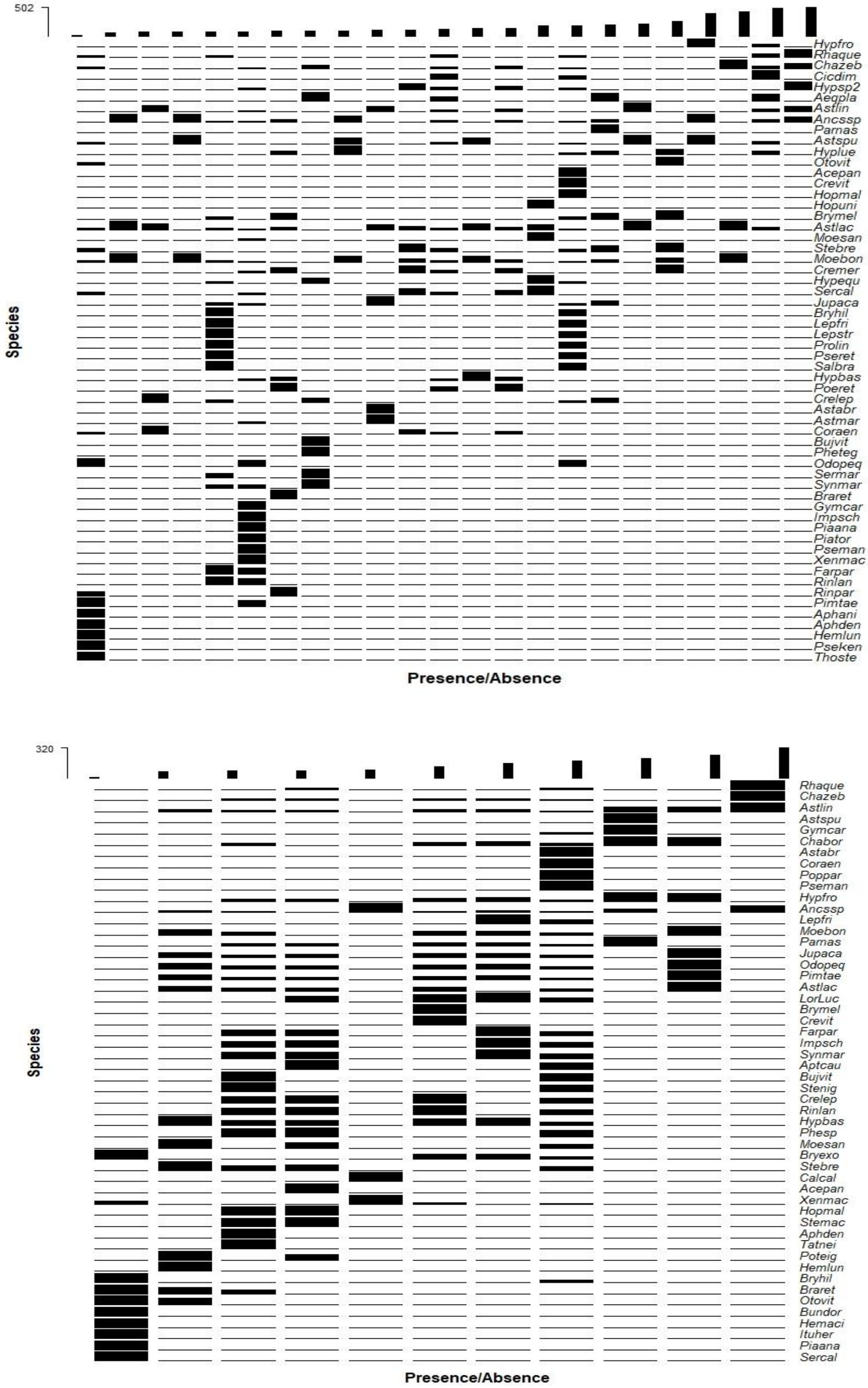

Figure 2 – Ordination of fish species (presence/absence) according to elevation gradient found on Serra da Bodoquena. Above, Formoso River drainage and Salobra River below. Each column representing a sample site. See Table 1 in Supplementary Material to species abbreviations. Source: Prepared by the author.

Figure 3 – Fish species contributed the most to community organization in Salobra river according to altitude. Upstream species: A. *Rhamdia quelen*, B. *Characidium zebra*, C. *Astyanax lineatus*; D. *Ancistrus* sp. Downstream species: E. *Brycon hilarii*; F. *Brachychalcinus retrospina*; G. *Otocinclus vittatus*; H. *Bunocephalus doriae*; I. *Hemiodontichthys acipenserinus*; J. *Ituglanis herberti*; K. *Piabarchus analis*; L. *Serrapinnus calliurus*. Source: Prepared by the author.

Functional traits

The first two axes of the PCA explained 36.2% of the variance in the ecomorphological data, with axis 1 accounting for 18% of the variation (Figure 4). The first was influenced by (Ops), (Osh), (Edst), (Fsf) and (logM) (eigenvalues =0.71, 0.66, 0.63, -0.1, -0.52, respectively; Table 2).

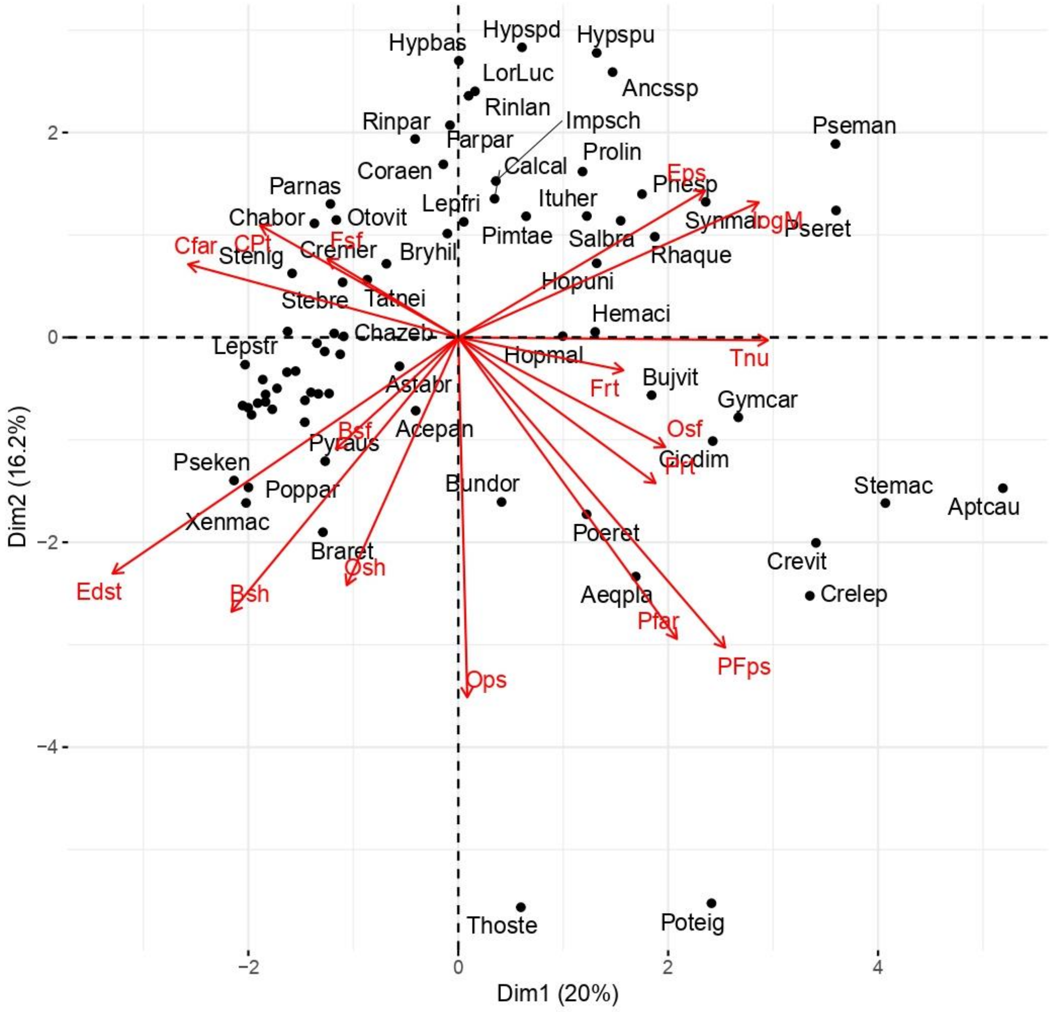

Figure 4 – Biplot resulting from Principal Component Analysis, showing species in black (species abbreviations in Table 1 in Supplementary Material) and functional attributes in red (see abbreviations in Table 1). Source: Prepared by the author.

Table 2 – Functional attributes and their eigenvalues from fish species of Serra da Bodoquena streams.

Functional attributes	**Dimension 1**	**Dimension 2**
Mouth-protrusion length (Prt)	0.1553607	0.40538784
Oral-gape surface (Osf)	0.4455739	0.12109956
Oral-gape shape (Osh)	0.6684870	-0.21963361
Oral-gape position (Ops)	0.7140655	0.04019007
Eye size (Edst)	0.6372954	-0.50275335
Eye position (Eps)	0.1746135	0.13978339
Body transversal shape (Bsh)	0.5376162	-0.19551385
Body transversal surface (Bsf)	0.4517834	-0.41240597
Pectoral-fin position (PFps)	0.4649102	0.74727934
Aspect ratio of the pectoral fin (PFar)	0.2452110	0.64601553
Caudal-peduncle throttling (CPt)	-0.1048708	-0.44838294
Aspect ratio of the caudal fin (CFar)	-0.1055099	-0.53804108
Fins surface ratio (Frt)	0.1503552	0.58807083
Fins surface to body size ratio (Fsf)	-0.1093350	-0.17673708
Body mass (logM)	-0.5227986	0.24627900

Beta-diversity

Overall, taxonomic and functional beta diversity and its components were higher in Formoso basin than Salobra (Figure 5, Table 3). The partitioning pattern was similar for both basins, wherein turnover was the main responsible for taxonomic beta diversity and nestedness was responsible for the majority of the functional beta diversity. Interestingly, in Salobra basin this pattern was more accentuated with almost of all functional beta diversity due to nestedness (Table 3).

Functional beta diversity (x̄βSOR) was better explained than taxonomic (R^2 adjFunc = 0.73; R^2 adjTaxo = 0.64). Taxonomic nestedness (x̄βSNE) was not explained by the altitude or deforestation gradients, while taxonomic turnover (x̄βSIM) was explained mainly by altitude in Salobra (p-value = 0.0235). Functional nestedness (R^2 adj = 0.44) was better explained than functional turnover (R² adj = 0.25), wherein altitude in Salobra strongly determined traits loss or gain. Thus, altitude in Salobra drove the replacement of species followed by the loss or gain of traits (Table 4). Despite showing lower beta diversity compared to Formoso, the altitude in Salobra basin led to the increase of the taxonomic and functional beta diversity by increasing turnover of species and loss and gain of traits.

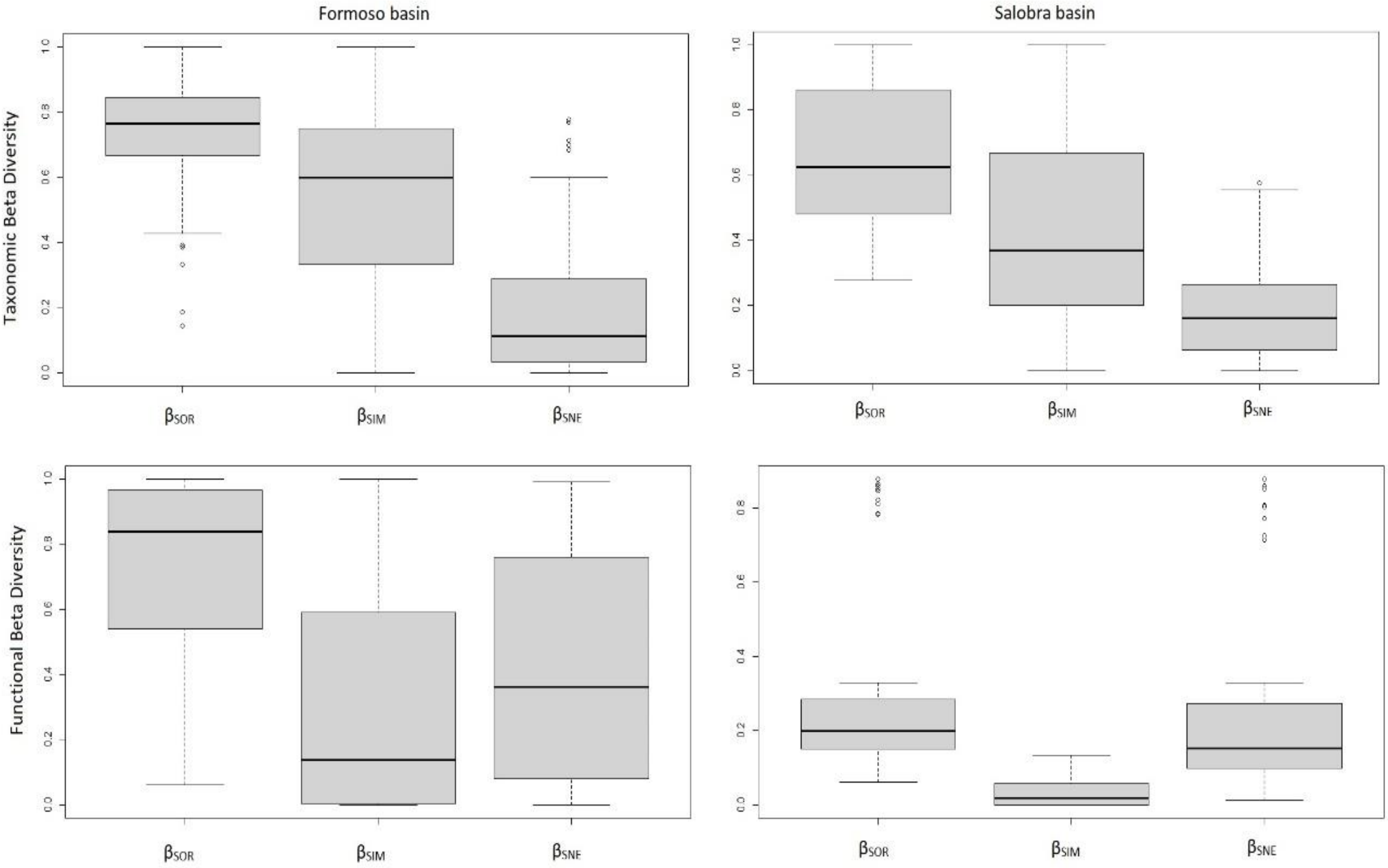

Figure 5 – Taxonomic (a) and functional (b) beta diversity (βSOR), turnover (βSIM) and nestedness (βSNE) of functional groups in Formoso and Salobra rivers drainages. Source: Prepared by the author.

Table 3 – Average and contribution (%) of taxonomic and functional spatial beta diversity (βSOR), turnover (βSIM) and nestedness (βSNE) for Formoso River drainage and Salobra River drainage, tributaries of Serra da Bodoquena system. In bold are the highest percentages.

	Taxonomic				**Functional**			
	Formoso		**Salobra**		**Formoso**		**Salobra**	
	Mean	**%**	**Mean**	**%**	**Mean**	**%**	**Mean**	**%**
βSOR	0.74		0.65		0.73		0.30	
βSIM	0.56	**76.0%**	0.46	**70.0%**	0.31	42.0%	0.03	10.0%
βSNE	0.18	24.0%	0.19	30.0%	0.42	**58.0%**	0.27	**90.0%**

Table 4 – Regression and explained deviance results between degree of natural (Altitude) and anthropic (Deforestation) gradients for temporal beta diversity (βSOR), turnover (βSIM) and nestedness (βSNE) for taxonomic and functional datasets.

		BetaSOR		**BetaSIM**		**BetaSNE**	
		F	**P-value**	**F**	**P-value**	**F**	**P-value**
Taxonomic	s(Altitude): Formoso	0.001	0.9760	0.112	0.7408	0.381	0.5420
	s(Altitude): Salobra	7.255	**0.0006**	3.765	**0.0235**	1.861	0.1870
	s(Deforestation): Formoso	0.084	0.8625	0.298	0.5897	0.682	0.4160
	s(Deforestation): Salobra	2.776	0.1081	0.287	0.5967	0.278	0.6020
	R^2(adj)	0.641		0.302		0.0332	
	Deviance explained	71.7%		42.7%		17.6%	
Functional	s(Altitude): Formoso	0.242	0.6270	0.565	0.4588	0.086	0.7713
	s(Altitude): Salobra	20.970	**<0.0001**	2.931	0.0596	18.787	**0.0002**
	s(Deforestation): Formoso	0.549	0.4650	0.050	0.8242	1.112	0.3439
	s(Deforestation): Salobra	0.006	0.9410	0.228	0.6368	1.379	0.2380
	R^2(adj)	0.736		0.254		0.446	
	Deviance explained	78%		36.9%		55.8%	

4.4 Discussion

In the present chapter, taxonomic and functional β-diversities of fish were analyzed in two basins from Serra da Bodoquena which differ in the elevation and land use history. Overall, the assemblage partitioning pattern was similar for both basins with high replacement of species and loss/gain of functional traits among the sites, and Formoso held highest values of the taxonomic and functional β-diversity. These high values can be a response to non-mutualistic exclusive niche-based factors, such as dispersal limitation between species (Püttker et al., 2015) and inter-specific competition (Götzenberger et al., 2012). From a landscape perspective, different sort of actions within the watershed contributes to a greater environmental heterogeneity which generates dissimilar levels of resource availability and consequently increase the uniqueness of species and traits sets among sites (Janzen & Schoener, 1968; Tucker et al., 2016). Notwithstanding, deterministic and stochastic processes can shape communities, with greater or lesser importance of one or the other process (Segre et al., 2014). In the case of the Serra da Bodoquena fish communities, although they belong to the same ecosystem in the broadest sense (karst streams), with altitude being an important factor, they are positioned in different drainages, each with its own history. In the Salobra basin, the deterministic role of altitude explains the lower taxonomic and functional beta diversity. These findings reflect, in a way, previous observations that deterministic changes can homogenize assemblages regionally (McKinney & Lockwood, 1999; Segre et al., 2014; Siqueira et al., 2015). On the other hand, stochastic processes can increase the differences in species composition between different sites (Segre et al., 2014). This role is demonstrated in the present chapter by the greater taxonomic and functional beta diversity in the Formoso set of streams.

Waterfalls represent physical barriers for fish movement (Buckup et al., 2000). In consequence, the accumulation of these physical filters along the longitudinal continuum tend to select traits responsible to pass through these barriers. Although Formoso and Salobra catchments are in the same altitude quotes, Salobra presents a steeper slope, with sequences of waterfalls, while Formoso presents a gentler slope. Thus, while no ordination of the community according to the altitude was observed to Formoso basin (Fig. 2), a congruent relation occurred in the Salobra basin, where the higher strata of Salobra River was represented by *Rhamdia quelen*, *Characidium zebra*, *Astyanax lineatus* and *Ancistrus* sp. In the lower quotes the species contributed the most were *Brycon hilarii*, *Brachychalcinus retrospina*, *Otocinclus vittatus*, *Bunocephalus doriae*, *Hemiodontichthys acipensericus*, *Ituglanis herberti*, *Piabarchus analis* and *Serrapinnus calliurus*. From the four species in the higher strata, which occurs near the river spring, *Characidium zebra*, *Astyanax lineatus* and *Ancistrus* sp. are high vagile species that rely on different set of traits and strategies to pass through the environmental filter, in this case, the successive waterfalls. *Characidium zebra* literally climb the waterfalls supported by rays of the pectoral and pelvic pairs of fins, as stated by Buckup et al. (2000). *Astyanax lineatus* uses the hydrodynamic shape, as well as the developed caudal peduncle and caudal fin, which are intimately related to habitat exploration in lotic systems (Kerfoot & Schaefer, 2006) to jump its way through the running waters. *Ancistrus* sp. uses the oral disk to climbing through sucking the substrate, a similar behavior exhibited by Andean suckermouths, such as Loricariidae and Astroblepidae species (Carvajal-Quintero et al., 2015), to colonize high slope streams. Curiously, *Rhamdia quelen* was between the species in higher strata. This slender bodied catfish species does not present adaptations to overcome the physical barriers such as waterfalls but its occurrence upstream may be a reflect of the subterranean ecosystems that connect different stretches and drainages through channels within the karst (see Cordeiro et al., 2013). The presence of these representants of four families (Characidae, Crenuchidae, Loricariidae and Heptapteridae) contrasts the founds in streams of Mata Atlântica where only Loricariidae were found on steeper sites (Caetano et al., 2021) suggesting that the diversity traits, which lead to a diversity of strategies, allows different species to colonize steeper areas in Serra da Bodoquena.

According to the River Continuum Concept (RCC), downstream characteristics are a response to changes in resource availability and, along which the biota, are predictably structured as a function of the joint of the adjacent riparian vegetation and upstream processes (Vannote et al., 1980). Furthermore, the slope of the streams may represent a barrier to dispersal which tend to select species and traits upstream. Hence, is expected that the fish assemblages from upstream represent a subset species pool in the catchment, generating a nested pattern of diversity (Caetano et al., 2021). While both basins demonstrated a nested pattern of functional β-diversity, taxonomic facet exhibited a turnover pattern, indicating that a conservative set of traits are better fitted to environmental constraints, but with changes in species composition across the fish assemblages. In the Salobra River, this pattern was associated to the elevation gradient which may reflect the configuration of the basin, with high steeper slope in the headwaters and flowing into the Pantanal floodplain. Thus, there is a replacement of fish species along the streams from headwater species to species from floodplain, but despite that, traits are conserved, probably because several species can share similar traits (i.e., functional redundancy). For example, upstream assemblages are represented by loricariid catfishes *Ancistrus* sp. and *Loricaria luciae*, while similar traits are found in *Otocinclus vittatus* and *Hemiodontichthys acipenserinus* in lower quotes. This turnover mirrors shift not only in the structure of the stream but also of physicochemical parameters, i.e., from a karst environment to a sedimentary basin. Indeed, pH variation is known to be a driver to turnover patterns in Upper Paraguay River basin headstreams (Nakamura et al., 2021). Thus, environmental filtering would be related not only to the selection of a similar set of morphological traits, but also to the selection of some physiological aspects of the species.

Deforestation plays a major role on fish distribution, since the vegetation removal leads to synergic effects of larger sun exposal, siltation, reduction of the flow and physicochemical changes. From the β-diversity perspective, substitution of native vegetation to agroecosystems causes communitie’s homogenization by filtering a set os species with a high redundancy of traits the whole basin (Casatti et al., 2015). In Serra da Bodoquena, Formoso and Salobra presented highly deforested rates, reaching 98.5% and 64% respectively, mostly due to the conversion of forests to pasture or crop fields. Interestingly, deforestation gradient was not related to changes in species composition or beta diversity patterns in both basins. This lack of correlation can be interpreted as a nonlinearity effect among the deforestation impact and changes in the stream biodiversity (Dala-Corte et al., 2020), especially in recently impacted areas. Brejão et al. (2018) found that negative threshold responses to deforestation and consequent loss of species in Amazonian streams occur at low levels (<20% of deforestation) while Valente-Neto et al. (2021) found significative changes in fish community after 48% of deforestation in the Serra da Bodoquena streams. Allied to this differences that can occur in the response to the spatial rates of deforestation, the effects of land use changes can present a delay of over ten years until significative changes in the fish community can be observed (Brejão et al., 2018). In fact, conversion of native areas or replacement of pastures to agroecosystems is a recent impact upon streams from Serra da Bodoquena, especially in the Formoso basin. Due the gentle slope and absence of public conservation units in this basin, the area of this watershed had a conversion to agroecosystems only around 2016 with an intense increase in the past three years. Thus, it is plausible to assume that fish communities from Formoso basin are going through a time-lag effect and biotic changes are expected to happen in a few years. Furthermore, the higher richness found in this basin can already be an indicative of disturbance, once that high diversity may be observed in unstable environments as a result of the joint of recently established, mature and declining populations (Reed, 1978). Although the results herein do not consider the diversity component of sampled sites, higher richness was already registered in streams surrounded by pasture in comparison to conserved streams in Serra da Bodoquena (Casatti et al., 2010). Considering this, we advocate that efforts to conserve and restore riparian forest in Formoso basin must be urgently done, because the effects of current impacts can only be seen in long-term. Thus, biodiversity loss in the future can be massive, especially from those sensitive species, that are usually functionally unique.

The mountainous terrain and difficult access to the areas where headwater streams occur are beneficial to the implementation of parks and reserves, especially by their degree of preservation (Barrela et al., 2014). Such areas can become a refuge area and, from the metacommunity perspective, source of species to unprotected areas, which endorses the function of these restricted environments as a valuable tool to environmental restoration processes. Moreover, in case of fish, the perennial cycle of streams allows one long-term environment and community stability compared to seasonally disturbed habitats. Thus, in Pantanal floodplain, where the flood stochastically dictates the colonization and extinction of fish populations across the habitats, Upper Paraguay River basin streams represent fundamental areas to preserve the diversity in the entire ecosystem. This is especially true in the current scenario, where sequential wildfires in Pantanal, caused by human activities, killed more than 17 million terrestrial vertebrates (Tomas et al., 2021) and where the direct and indirect effects of this impact on fish communities' dynamics at short and long-term are still uncertain. Notwithstanding, Pantanal domain have lost 74% of water surface from 1985 to 2020 (Watanabe, 2021), which represents the highest water loss among all Brazilian biomes. Thus, conservation of Serra da Bodoquena streams and their associated biota represents a likely refugia and a source of fish populations to the entire basin. However, despite the establishment of the PNSB in the region, headwaters of Salobra river basin are outside of the park boundaries, and consequently exposed to several anthropic impacts, such as the siltation of the streambed, as observed by Vilela et al. (2020). Moreover, protection in Formoso basin is restricted to small private natural heritage reserves, without a general consensus about the watershed conservation. Most worrying, as stated by Frederico et al. (2018), protected areas in Amazon basin fails to protect stream-dwelling species. This is especially concerning because while 43% of Brazilian Amazon is formally protected, only 2.5% of the Upper Paraguay River basin area is within conservation units, mostly, in the lowlands (Harris et al., 2005). Furthermore, in Serra da Bodoquena, despite the income resulted by ecotourism activities, protection of the environment and its fauna are not always achieved. For instance, Bonito city which concentrates most of the tourist attractiveness and income, also holds the first position in the loss of Mata Atlântica in Brazil (SOS MA, 2021). In conclusion, conservation of streams of Serra da Bodoquena represents not just an economic maintenance of tourism in the region, but as a hotspot to the biodiversity in the Upper Paraguay River basin and a possible refugia for the Pantanal systems.

4.5 References

Angermeier, P. L. & J. R. Karr, 1984. Fish communities along environmental gradients in a system of tropical streams. Environmental Biology of Fishes 9: 117–135.

Angermeier, P. L. & I. J. Schlosser, 1989. Species-area relationships for stream fishes. Ecology 70:14501642.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134–143.

Bareswill R., B. Golla, M. Streloke & R. Schulz, 2013. Entry and toxicity of organic pesticides and copper in vineyard streams: erosion rills jeopardise the efficiency of riparian buffer strips. Agriculture, Ecosystems and Environment 146: 81–92.

Barrella, W., Martins, A.G., Petrere, M. et al., 2014. Fishes of the southeastern Brazil Atlantic Forest. Environmental Biology of Fishes 97: 1367–1376.

Beukhof, E., T. Dencker, L. Pecuchet & M. Lindegren, 2019. Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Marine Ecology Progress Series 610: 205–222.

Brejão, G. L., D. J. Hoeinghaus, M. A. Pérez-Mayorga, S. F. B. Ferraz & L. Casatti, 2018. Threshold responses of Amazonian stream fishes to timing and extent of deforestation. Conservation Biology 32: 860–871.

Britski H. A., K. Z. S. Silimon, B. S. Lopes, 2007. Peixes do Pantanal. Manual de identificação. 2ed. Brasília, Embrapa. 227p.

Buckup P. A., C. Zamprogno, F. Vieira & R. L. Teixeira, 2000. Waterfall climbing in *Characidium* (Crenuchidae: Characidiinae) from estearn Brazil. Ichthyological Exploration of Freshwaters 11(3): 273–278.

Carvajal-Quintero J. D., J. A. Maldonaldo-Campo & A. Urbano-Bonilla, 2015. Climbing behavior of *Cordylancistrus* sp. in the Colombian Andes. Universitas Scientiarum 20(2): 209–215.

Carvalho, R. A. & F. L. Tejerina-Garro, 2015. Environmental and spatial processes: what controls the functional structure of fish assemblages in tropical rivers and headwater streams? Ecology of Freshwater Fish 24: 317–328.

Casatti, L. & R. M. C. Castro, 1998. A fish community of the São Francisco River headwater riffles, southeastern Brazil. Ichthyological Exploration of Freshwaters 9: 229–242.

Casatti, L., R. M. Romero, F. B. Teresa, J. Sabino & F. Langeani, 2010. Fish community structure along a conservation gradient in Bodoquena Plateau streams, central West of Brazil. Acta Limnologica Brasiliensia 22: 50–59.

Casatti, L., F. B. Teresa, J. O. Zeni, M. D. Ribeiro, G. L. Brejão, M. Ceneviva-Bastos, 2015. More of the same: high functional redundancy in stream fish assemblages from tropical agroecosystems. Environmental Management 55:1300–14.

Castro, R. M. C, 2021. Evolução da ictiofauna de riachos sul-americanos (Castro, 1999) revisitado após mais de duas décadas. Oecologia Australis 25(2): 231–245.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine & S. W. Kembel, 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12: 693–715.

Chaves J., C. Neill, S. Germer, S. G. Neto, A. Krusche & H. Elsenbeer, 2007. Land management impacts on runoff sources in small Amazon watersheds. Hydrological Processes 22(12): 1766–1775.

Cordeiro L. M., R. Borghezan & E. Trajano, 2013. Distribuição, riqueza e conservação dos peixes troglóbios da Serra da Bodoquena, MS (Teleostei: Siluriformes). Revista da Biologia 10(2): 21–27.

Costa M. H., A. Botta & J. A. Cardille, 2003. Effects of large-scale changes in land cover on the discharge of the Tocantins River, Southeastern Amazonia. Journal of Hydrology 283(1): 206–217.

Dala-Corte, R. B., L. F. Sgarbi, F. G. Becker & A. S. Melo, 2019. Beta diversity of stream fish communities along anthropogenic environmental gradients at multiple spatial scales. Environmental Monitoring and Assessment 191: 288.

Dala-Corte, R. B., A. S. Melo, T Siqueira, L. M. Bini, R. T. Martins, A. M. Cunico, C. S. Monteiro-Júnior et al., 2020. Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region. Journal of Applied Ecology 57(7): 1391–402.

Davis, T. L. O, 1988. Temporal changes in the fish fauna entering a tidal swamp system in tropical Australia. Environmental Biology of Fishes 21: 161–172.

Dolédec, S. & B. Stazner, 2010. Responses of freshwater biota to human disturbances: contribution of J-NABS to developments in ecological integrity assessments. Journal of the North American Benthological Society 29: 286–311.

Dumay O., P. S. Tari, J. A. Tomasini & D. Mouillot, 2004 Functional groups of lagoon fish species in Languedoc Roussillon, southern France. Journal of Fish Biology 64: 970–983.

Dudgeon, D., 2019. Multiple threats imperil freshwater biodiversity in the Anthropocene. Current Biology 29: R960–R967.

Ekroos, J., J. Heliölä & Kuussaari, M, 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. Journal of Applied Ecology 47: 459–467.

Frissell, C. A., W. J. Liss, C. E. Warren & M. D. Hurley, 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10: 199–214.

Froehlich, O., 2010. Ictiofauna de um córrego na Serra da Bodoquena: Estrutura, Variações Longitudinal e Temporal e Efeitos sobre Comunidades Bentônicas. Tese de doutorado. Universidade Federal de Mato Grosso do Sul.

Gatz, A. J., 1979. Community organization in fishes as indicated by morphological features. Ecology 60: 711–718.

Glova, G. & M. J. Duncan, 1985. Potential effects of reduced flows on fish habitats in a large braided river, New Zealand. Transactions of the American Fisheries Society 114: 165–181.

Götzenberger, L., F. de Bello, K. A. Brathen, J. Davison, A. Dubuis, A. Guisan, A., et al., 2012. Ecological assembly rules in plant communities – Approaches, patterns and prospects. Biological Reviews 87: 111–127.

Hastie, T. & R. Tibshirani, 1993. Varying-coefficient models. Journal of the Royal Statistical Society, Series B: Statistical Methodology 55: 757–796.

Heino, J., A. S. Melo, L. M. Bini, 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshwater Biology 60(2): 223–235.

Helfman, G. S, 1981. Twilight activities and temporal structure in a freshwater fish community. Canadian Journal of Fisheries and Aquatic Sciences 38: 1405–1420.

Holmlund, C. M. & M. Hammer, 1999. Ecosystem services generated by fish populations. Ecological Economics 29(2): 253–268.

Horn, M. H., S. B. Correa, P. Parolin, B. J. A. Pollux, J. T. Anderson, C. Lucas, P. Widmann, A. Tjiu, M. Galetti, M. Goulding, 2011. Seed dispersal by fishes in tropical and temperate fresh waters: The growing evidence. Acta Oecologica 37(6): 561–577.

ICMBIO (Instituto Chico Mendes de Conservação da Biodiversidade), 2013. Plano de manejo do Parque Nacional da Serra da Bodoquena. Encarte 3 – Análise do PNSB. Available at www.icmbio.gov.br/portal/images/stories/docs-planos-de-manejo/Encarte3_serra_da_bodoquena.pdf

Jackson, D. A., 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74: 2204-2214.

Janzen, D. H., & T. W. Schoener, 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49: 96–110.

Karp, D. S., A. J. Rominger, J. Zook, J. Ranganathan, P. R. Ehrlich, & G. C. Daily, 2012. Intensive agriculture erodes beta-diversity at large scales. Ecology Letters 15: 963–970.

Karpouzi V.S. & K. I. Stergiou, 2003. The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. Journal of Fish Biology 62: 1353–1365.

Kerfoot J. R. & J. F. Schaefer, 2006. Ecomorphology and habitatutilization of *Cottus* species. Environmental Biology of Fishes 76:1–13.

Landeiro V.L., C. A. Zucco, G. Oliveira-Santos & J. F. S. Menezes, 2013. Introdução ao uso do programa R. Manaus: Instituto Nacional de Pesquisas da Amazônia.

Leitão, R.P., J. Zuanon, S. Villéger, S. E. Williams, C. Baraloto, C. Fortunel, F. P. Mendonça & D. Mouillot, 2016. Rare species contribute disproportionately to the functional structure of species assemblages. Proceedings of the Royal Society B: Biological Sciences 283: 20160084.

Macarthur R. & R. Levins, 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101: 377–385.

Mahon, R., 1984. Divergent structure in fish taxocenes of north temperate streams. Canadian Journal of Fisheries and Aquatic Sciences 41: 330–350.

Mason, N. W., D. Mouillot, W. G. Lee & J. B. Wilson, 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111: 112–118.

McKinney, M. L. & J. L. Lockwood, 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14: 450–453.

Merten G. H. & J. P.G. Minella, 2013. The expansion of Brazilian agriculture: Soil erosion scenarios. International Soil and Water Conservation Research 1(3): 37–48.

Merten G. H., J. P. G. Minella, M. Moro & C. Maier, 2010. Expansion of Brazilian Agricultural Territory: Changes in Land Use. Advances in Geoecology, 41: 13–21.

Mouillot, D., O. Dumay & J. A. Tomasini, 2007. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. Estuarine, Coastal and Shelf Science 71: 443–456.

Nakamura, G., W. Vicentin & Y. R. Súarez, 2021. Taxonomic and phylogenetic beta diversity in headwater stream fish communities of the Paraná and Paraguai River basins. Neotropical Ichthyology 19(01): e200126.

Ortega, J. C. G., R. M. Dias, A. C. Petry, E. F. Oliveira & A. A. Agostinho, 2015. Spatio-temporal organization patterns in the fish assemblages of a Neotropical floodplain. Hydrobiologia 745: 31–41.

Poff, N. L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16: 391-409.

Püttker, T., A. A. Bueno, P. I. Prado, & R. Pardini, 2015. Ecological filtering or random extinction? Beta-diversity patterns and the importance of niche-based and neutral processes following habitat loss. Oikos 124: 206–215.

Rahbek, C., 1995. The elevational gradient of species richness—a uniform pattern. Ecography 18: 200–205.

Ramankutty, N., A. T. Evan, C. Monfreda & J. A. Foley, 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Global Biogeochemical Cycles 22: GB1003.

Reed, C, 1978. Species diversity in aquatic microecosystems. Ecology 59: 481-488.

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

Ribeiro, M. D., F. B. Teresa & L. Casatti, 2016. Use of functional traits to assess changes in stream fish assemblages across a habitat gradient. Neotropical Ichthyology 14(1), 1–10.

Roa-Fuentes, C. A., J. Heino, M. V. Cianciaruso, S. Ferraz, J. O. Zeni & L. Casatti, 2019. Taxonomic, functional, and phylogenetic β-diversity patterns of stream fish assemblages in tropical agroecosystems. Freshwater Biology 64(3): 447–460.

Roberts, J. H. & N. P. Hitt, 2010. Longitudinal structure in temperate stream fish communities: evaluating conceptual models with temporal data. American Fisheries Society Symposium 73: 281–289.

Sallun Filho W & I. Karmann, 2007. Geomorphological map of the Serra da Bodoquena karst, west-central Brazil. Journal of Maps 3: 282–295.

Schwartz J. S. & E. E. Herricks, 2008. Fish use of ecohydraulic-based mesohabitat units in a low-gradient Illinois stream: Implications for stream restoration. Aquatic Conservation: Marine and Freshwater Ecosystems 18: 852–866.

Scott M. C. & G. S. Helfman, 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26: 6–15.

Segre, H., R. Ron, N. Malach, Z. Henkin, M. Mandel & R. Kadmon, 2014. Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. Ecology Letters 17: 1400–1408.

Sibbing F.A. & L. A. J. Nagelkerke, 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. Reviews in Fish Biology and Fisheries 10: 393–437.

Siqueira, T., C. Lacerda & V. S. Saito, 2015. How does landscape modification induce biological homogenization in Tropical stream metacommunities? Biotropica 47: 509–516.

Smith, C. L., & C. R. Powell, 1971. The summer fish communities of Brier Creek, Marshall County, Oklahoma. American Museum Novitates 2458: 1–30.

Socolar, J. B., J. J. Gilroy, W. E. Kunin & D. P. Edwards, 2015. How should beta-diversity inform biodiversity conservation? Trends in Ecology & Evolution 31: 67–80.

SOS Mata Atântica (SOS MA), 2021. Aqui tem mata? Available at https://www.aquitemmata.org.br/#/

Tomas W. M., C. N. Berlink, R. M. Chiaravalotti, et al., 2021. Counting the dead: 17 million vertebrates directly killed by the 2020’s wildfires in the Pantanal wetland, Brazil. Research Square. 10.21203/rs.3.rs-859794/v1

Trenkel, V. M., J. K. Pinnegar, W. A. Dawson, M. H. du Buit & A. N. Tidd, 2005. Spatial and temporal structure of predator–prey relationships in the Celtic Sea fish community. Marine Ecology Progress Series 299: 257-268.

Tscharntke T, A. M. Klein, A. Kruess, I. Steffan-Dewenter & C. Thies, 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecology Letters 8: 857–874.

Tucker, C. M., L. G. Shoemaker, K. F. Davies, D. R. Nemergut, & B. A. Melbourne, 2016. Differentiating between niche and neutral assembly in metacommunities using null models of β-diversity. Oikos 125: 778–789.

Valente-Neto, F., B. T. Martínez, R. M. Hughes, A. Ferreira, F. Severo-Neto, F. L. Souza, R. P. Souza, S. C. Escarpinati & F. O. Roque, 2021. Incorporating costs, thresholds and spatial extents for selecting stream bioindicators in an ecotone between two Brazilian biodiversity hotspots, Ecological Indicators 127: 107761.

Verberk W. C., C. G. E. Van Noordwijk & A. G. Hildrew, 2013. Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. Freshwater Science 32: 531–547.

Vilela, M. J. A., F. Severo-Neto, O. Froehlich & F. R. Carvalho, 2021. Ictiofauna do Parque Nacional da Serra da Bodoquena, Mato Grosso do Sul, Brasil: composição e subsídios à conservação. Biotemas 34(2): 1–23.

Villéger, S., J. R. Miranda, D. F. Hernandez & D. Mouillot, 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecological Applications 20: 1512–1522.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier, 2007. Let the concept of trait be functional!. Oikos 116: 882–892.

Watanabe, P, 2021. Pantanal perde 74% da água desde 1985, e pesquisadores dizem que Brasil está secando. Folha de São Paulo. Available at https://www1.folha.uol.com.br/ambiente/2021/08/pantanal-perde-75-da-agua-desde-1985-e-pesquisadores-dizem-que-brasil-esta-secando.shtml

Watson, D. J. & E. K. Balon, 1984. Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. Journal of Fish Biology 25: 371–384.

Webb, P. W., 1984. Form and function in fish swimming. Scientific American 251: 72–82.

Whittaker, R. J. & J. M. Fernández-Palacios, 2007. Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, Oxford.

Wood, S., 2021. Package “mgcv”. Mixed GAM computation vehicle with automatic smoothness estimation. Available at https://cran.r-project.org/web/packages/mgcv/mgcv.pdf

Zeni, J. O., D. J. Hoeinghaus, C. A. Roa-Fuentes & L. Casatti, 2020. Stochastic species loss and dispersal limitation drive patterns of spatial and temporal beta diversity of fish assemblages in tropical agroecosystem streams. Hydrobiologia 847: 3829–3843.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev & G. M. Smith, 2009. GLM and GAM for absence-presence and proportional data Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health, Springer Verlag. pp. 1–15

4.6 Supplementary material

Table 1 – List of fish species from Serra da Bodoquena streams, divided by drainages. Codes for each species are presented below.

Taxa	**Codes**	**Drainages**	
		Formoso	**Salobra**
CHARACIFORMES			
Parodontidae			
Parodon nasus Kner, 1859	parnas	X	X
Curimatidae			
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)	stebre	X	X
Steindachnerina nigrotaenia (Boulenger, 1902)	stenig		X
Prochilodontidae			
Prochilodus lineatus Valenciennes, 1836	prolin	X	X
Anostomidae			
Leporinus friderici Bloch, 1794	lepfri	X	X
Leporinus striatus Kner, 1858	lepstr	X	
Crenuchidae			
Characidium borellii (Boulenger, 1895)	chabor		X
Characidium aff. *zebra* Eigenmann, 1909	chazeb	X	X
Gasteropelecidae			
Thoracocharax stellatus (Kner, 1858)	thoste	X	
Characidae			
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	aphani	X	
Aphyocharax dentatus Eigenmann and Kennedy, 1903	aphden	X	X
Astyanax abramis (Jenyns, 1842)	astabr	X	X
Astyanax lacustris (Lütken, 1875)	astlac	X	X
Astyanax lineatus (Perugia, 1891)	astlin	X	X
Astyanax marionae Eigenmann, 1911	astmar	X	
Astyanax sp. 1	astspu	X	
Brachychalcinus retrospina Boulenger, 1892	braret	X	X
Brycon hilarii (Valenciennes, 1850)	bryhil	X	X
Bryconamericus exodon Eigenmann, 1908	bryexo		X
Bryconops melanurus (Bloch, 1794)	brymel	X	X
Creagrutus meridionalis Vari & Harold, 2001	cremer	X	
Deuterodon luetkenii (Boulenger, 1887)	hyplue	X	
Hemigrammus lunatus Durbin, 1918	hemlun	X	X
Hyphessobrycon eques Steindachner, 1882	hypequ	X	
Jupiaba acanthogaster (Eigenmann, 1911)	jupaca	X	X
Moenkhausia bonita Benine, Castro & Sabino, 2004	moebon	X	X
Moenkhausia oligolepis (Günther, 1864)	moeoli	X	X
Odontostilbe pequira (Steindachner, 1882)	odopeq	X	X
Phenacogaster tegatus (Eigenmann, 1911)	pheteg	X	

Piabarchus analis (Eigenmann, 1914)	piaana	X	X
Piabarchus torrenticola Mahnert & Géry, 1988	piator	X	
Poptella paraguayensis (Eigenmann, 1907)	poppar		X
Psellogrammus kennedyi Eigenmann, 1903	pseken	X	
Salminus brasiliensis (Cuvier, 1816)	salbra	X	
Serrapinnus calliurus (Boulenger, 1900)	sercal	X	X
Serrasalmus marginatus Valenciennes, 1837	sermar	X	
Xenurobrycon macropus Myers & Miranda Ribeiro, 1945	xenmac	X	X
Acestrorhynchidae			
Acestrorhynchus pantaneiro Menezes, 1992	acepan	X	X
Erythrinidae			
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	hopuni	X	
Hoplias malabaricus (Bloch, 1794)	hopmal	X	X
Lebiasinidae			
Pyrrhulina australis Eigenmann & Kennedy, 1903	pyraus	X	
SILURIFORMES			
Aspredinidae			
Bunocephalus doriae Boulenger, 1902	bundor		X
Trichomycteridae			
Ituglanis herberti (Miranda Ribeiro, 1940)	ituher		X
Callicththyidae			
Callichthys callichthys (Linneaus, 1758)	calcal		X
Corydoras aeneus (Gill, 1858)	coraen	X	X
Loricariidae			
Ancistrus sp.	ancsp	X	X
Farlowella paraguayensis Retzer and Page, 1997	farpar	X	X
Hemiodontichthys acipenserinus (Kner, 1853)	hemaci		X
Hypostomus basilisko Tencatt, Zawadzki & Froehlich, 2014	hypbas	X	X
Hypostomus froehlichi Zawadzki, Nardi & Tencatt, 2021	hypfro	X	X
Hypostomus sp. 2	hypespd	X	
Loricaria luciae Thomas, Rodriguez, Cavallaro, Froehlich & Castro, 2013	lorluc		X
Otocinclus vittatus Regan, 1904	otovit	X	X
Rineloricaria lanceolata (Günther, 1868)	rinlan	X	X
Rineloricaria parva (Boulenger, 1895)	rinpar	X	
Pseudopimelodidae			
Pseudopimelodus mangurus (Valenciennes, 1835)	pseman	X	X
Heptapteridae			
Imparfinis schubarti (Gomes, 1956)	impsch	X	X
Phenacorhamdia sp.	phesp		X
Pimelodella taenioptera Ribeiro, 1914	pimtae	X	X
Rhamdia quelen (Quoy & Gaimard, 1824)	rhaque	X	X

Pimelodidae			
Pseudoplatystoma reticulatum Eigenmann & Eigenmann, 1889	pseret	X	
Auchenipteridae			
Tatia neivai (Ihering, 1930)	tatnei	X	X
GYMNOTIFORMES			
Gymnotidae			
Gymnotus carapo Linnaeus, 1758	gymcar	X	X
Sternopygidae			
Sternopygus macrurus (Bloch and Schneider, 1801)	stermac		X
Apteronotidae			
Apteronotus caudimaculosus de Santana, 2003	aptcau		X
CYPRINODONTIFORMES			
Poeciliidae			
Poecilia reticulata Peters, 1859	poeret	X	
BELONIFORMES			
Belonidae			
Potamorrhaphis eigenmanni Ribeiro, 1915	poteig		X
SYNBRANCHIFORMES			
Synbranchidae			
Synbranchus marmoratus Bloch, 1795	synmar	X	X
CICHLIFORMES			
Cichlidae			
Aequidens plagiozonatus Kullander, 1984	aeqpla	X	
Bujurquina vittata (Heckel, 1840)	bujvit	X	X
Cichlasoma dimerus (Heckel, 1840)	cicdim	X	
Crenicichla lepidota Heckel, 1840	crelep	X	X
Crenicichla vittata Heckel, 1840	crevit	X	X

5 Synthesis

Despite holding the status of one of the most well-conserved biomes, the future of the Pantanal is uncertain. In the plain, extreme annual wildfires and shifting on the flooding pulses can generate cascading processes which consequences still unknown. Besides, the highlands that harbors the headwater streams are threatened with siltation by erosion, agrochemicals and sewage input. In this sense, the knowledge of habits and distribution of fishes from Upper Paraguay River basin makes a fundamental tool not only upon a current conservation perspective, but also for restoration purposes.

Serra da Bodoquena has the potential to become a landmark in terms of stream's conservation and, from the ecosystem perspective, a source area to metapopulations across the entire basin, especially to small sized fish. During prolonged drought seasons in the Pantanal floodplain, the habitats that holds small species, as *baías*, dry completely, extinguishing, albeit on a small scale, populations of several fish species. In fact, a single *baía* can harbor more than a third of the amount of the species in the entire basin. Therefore, these habitats are true repositories of diversity and genetic pool of fishes which, in turn, plays essential roles on the ecosystem dynamics. However, while knowledge about ecosystem services of fish as fruit-eating and seed dispersal, prey-predator and host-parasite, and their relationships in the water-land interface still on its early years, the effects of climate change already can be seen in the Pantanal landscape. Consecutive dry seasons in the last years dried a large amount of *baías*, consequently driving to the loss of diversity and fish abundance in the environment. In this sense, the maintenance of small streams, which tend to be perennial, can be a key to avoid the simplification of fish communities in the Pantanal as a whole.

This Thesis sheds light not only about habitat use, resource partitioning and distribution of fishes from Serra da Bodoquena, but how interesting and underestimate fishes of Upper Paraguay River basin can be. We found that the set of fish species in Serra da

Bodoquena presents unique patterns of habitat use, which mirror the environmental imposition of the region, mostly altitude. The fish fauna is composed mainly by small fish that use margins and represent the largest portion of the richness of the community. Feeding partitioning is high and feeding is highly dependent on allochthonous items. In the context of the Upper Paraguay River basin, the region's unique altitude pattern is a critical factor in maintaining fish diversity among sites.

unesp UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
Campus de São José do Rio Preto

TERMO DE REPRODUÇÃO XEROGRÁFICA

Autorizo a reprodução xerográfica do presente Trabalho de Conclusão, na íntegra ou em partes, para fins de pesquisa.

São José do Rio Preto, 11/11/2021

Assinatura do autor