

Instituto Nacional de Pesquisas da Amazônia – INPA

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A ICTIOFAUNA DO INTERFLÚVIO PURUS-MADEIRA E OS FATORES ESTRUTURANTES EM
MÚLTIPLAS ESCALAS

Lis Fernandes Stegmann

Manaus, Amazonas
Novembro, 2019

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MÚLTIPLAS ESCALAS

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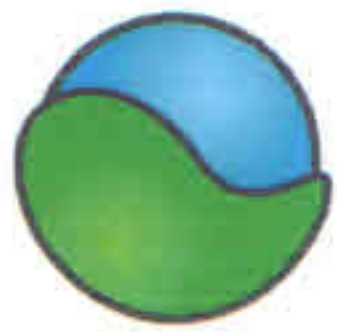
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Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

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Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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Coordenação PPG-ECO/INPA

Dedico esta tese ao meu pai, William Stegmann, cuja jornada pela Amazônia na década de 80 ainda reverbera no meu caminhar por essa imensidão.

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Resumo

O objetivo desta tese foi ampliar o nível de conhecimento sobre a fauna de peixes de riacho do interflúvio Purus-Madeira e compreender quais os principais gradientes ecológicos que atuam na estruturação das assembleias, incorporando tanto escalas espaciais quanto temporais. No **primeiro capítulo** nós apresentamos uma lista de ocorrência dos peixes de riacho do interflúvio Purus-Madeira, construída a partir de novas expedições às drenagens de difícil acesso e também através da incorporação dos registros previamente listados para a região. A lista final foi composta por 184 espécies, das quais 43 foram apenas coletadas na nossa amostragem e cinco gêneros representam novos registros para a bacia do rio Madeira. O número de espécies registradas é maior do que aqueles usualmente encontrados em outros estudos de riachos na Amazônia e sugere que a região abriga uma biodiversidade cujos fatores estruturantes ainda precisam ser melhor compreendidos. No **segundo capítulo** nós buscamos compreender como os padrões de diversidade taxonômica e funcional das assembleias de peixes de riacho são influenciados por variáveis locais e da paisagem. Nossos resultados mostram que em amplas escalas geográficas, a distância aos grandes rios é mais importante que a distância por água e que as condições ambientais na determinação de dissimilaridade taxonômica e funcional de assembleias e que riachos mais isolados tendem a ter menos espécies e menos diversidade funcional. No **terceiro capítulo**, nós analisamos a variação interanual da composição das assembleias de peixes de 11 riachos intermitentes do interflúvio Purus-Madeira. A composição das assembleias foi bastante variável entre anos, entretanto os riachos mais conectados com a planície de inundação apresentaram assembleias mais estáveis e compartilharam mais espécies entre anos, enquanto que as assembleias mais afastadas apresentam alta substituição de espécies ao longo do período analisado. Nossos resultados são um indício de que essas assembleias são estruturadas tanto por processos estocásticos de dispersão e extinção local, quanto pela influência das dinâmicas de recrutamento da planície de inundação.

Abstract

The goal of this study was to increase our knowledge about the stream-fish fauna of Purus-Madeira Interfluvie and evaluate the main ecological gradients that act in the assemblages structuring, incorporating both spatial and temporal scales. In the **first chapter** we present a checklist of stream-fish of Purus-Madeira Interfluvie, built up from new expeditions to difficult-to-access drainages and also by incorporating the previously listed records for the region. The final list consisted of 184 species, of which 43 were only collected in our samples and five genera represent new records for the Madeira River basin. The number of species recorded is higher than those usually found in other stream studies in the Amazon and suggests that this region harbor a biodiversity whose structuring factors still need to be better understood. In the **second chapter** we seek to understand how the taxonomic and functional diversity patterns of stream fish assemblages are influenced by local and landscape variables. Our results indicate that, at large spatial scales, distance to large rivers is more important than distance among sites and local conditions in explaining functional and taxonomic diversity of fish assemblages and more isolated streams tend to have fewer species and less functional diversity. In the **third chapter**, we analyze the interannual variation in the composition of fish assemblages of 11 intermittent streams of the Purus-Madeira Interfluvie. The composition of the assemblages was quite variable between years, however the streams more connected with the floodplain presented more stable assemblages and shared more species between years, while the most distant assemblages present high species substitution over the analyzed period. Our results provides a clue that these assemblages are structured both by stochastic processes of dispersion and local extinction, and by the recruitment dynamics of the floodplain.

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Artigo 2

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INTRODUÇÃO

A bacia Amazônica concentra a maior diversidade de peixes de água doce do mundo e abriga mais de um terço da ictiofauna conhecida para a região Neotropical, que abrange as Américas do Sul e Central (Reis *et al.* 2003). Aproximadamente 2.500 espécies de peixes já foram descritas e estima-se que o número de espécies seja muito maior, já que diversas drenagens permanecem pouco estudadas, devido a grande extensão da bacia e a dificuldade de acesso às drenagens mais isoladas, distantes dos grandes rios e dos centros urbanos (Lowe-McConnell 1999; Winemiller *et al.* 2008; Queiroz *et al.* 2013).

Essa alta diversidade de peixes reflete a grande heterogeneidade tanto de recursos quanto de ambientes aquáticos disponíveis e processos complexos de diversificação, devido a rica história geomorfológica da bacia (Albert & Reis 2011; Dagosta & Pinna 2017). Grande parte desta diversidade está concentrada nos pequenos corpos d'água que drenam as áreas de floresta, conhecidos localmente como riachos de terra-firme ou igarapés, e que representam uma das maiores e mais complexas redes hidrológicas do mundo (Junk 1989). A ictiofauna nesses ambientes é composta principalmente por espécies de pequeno porte bastante especializadas (Sabino & Zuanon 1998) e que, de modo geral, possuem baixa capacidade de dispersão, o que reduz o fluxo gênico entre populações e gera processos de endemismo e mudanças de composição mesmo em curtas distâncias (Castro 1999; Reis *et al.* 2016).

Nos últimos anos diversos pesquisadores se debruçaram sobre a rica fauna desses ambientes e sobre os processos ecológicos que determinam a ocorrência das espécies em finas escalas (Silva 1993; Sabino & Zuanon 1998; Bührnheim & Cox-Fernandes 2001; Mendonça *et al.* 2005; Pazin *et a.* 2006; Espírito-Santo *et al.* 2009; Couto *et al.* 2017). No entanto, grande parte dos estudos foi conduzido em drenagens próximas aos centros urbanos, enquanto que, informações sobre a composição de espécies de riachos mais distantes dos grandes rios, sobretudo nos interflúvios da calha sul da bacia amazônica, ainda são insuficientes.

Os interflúvios dos rios Juruá, Purus e Madeira estão inseridos na Formação Içá, que constitui formações tabulares, com grandes terraços fluviais e de fraca incisão de drenagens, provavelmente originada durante o Pleistoceno (CPRM 1997). Classificado por Sombroek (2000) como “planícies argilosas” (ou *loamy plains*), essas regiões apresentam terreno bastante plano e composto principalmente por silte e areia fina, o que resulta em solos mal drenados e de baixa estabilidade estrutural. O interflúvio Purus-Madeira, de aproximadamente 800 km extensão e 150 km de largura, abriga uma ampla heterogeneidade de habitats, incluindo diferentes tipos vegetacionais, como florestas de terra-firme, florestas alagadas e campinaranas (Rapp Py-Daniel *et al.* 2007). Expedições realizadas nos últimos anos pelos projetos GEOMA, PPBio e WCS BR-319 encontraram uma grande diversidade de espécies na região e registros de endemismo para diversos grupos biológicos, que se deve principalmente ao complexo mosaico de fisionomias presentes (Cohn-Haft *et al.* 2007; Rapp Py-Daniel *et al.* 2007; Bührnheim *et al.* 2008; Rohe *et al.* 2009).

Estudos sobre a composição e distribuição das espécies de peixes estão restritos a poucos trechos do interflúvio ou a riachos próximos a calha principal dos grandes rios (Rapp Py-Daniel *et al.* 2007; Barros *et al.* 2011; Queiroz *et al.* 2013; Vieira *et al.* 2016). Além disso, muitas espécies registradas por Barros *et al.* (2011) e por Vieira *et al.* (2016) não apresentaram status taxonômico completamente definido, o que demonstra a falta de informações precisas sobre os grupos taxonômicos que ocorrem nestas drenagens. Há também uma considerável lacuna amostral nas drenagens da porção central do interflúvio, que constituem centenas de igarapés, cujas nascentes se encontram sob influência da rodovia federal BR-319, que comunica Manaus com Humaitá e Porto Velho. A estrada de aproximadamente 800 km, foi construída no início da década de 70, porém a falta de manutenção fez com que, no fim da década de 80, a rodovia parasse oficialmente de funcionar e atualmente ela é intransitável em grande parte do seu percurso. Nos últimos anos, o governo brasileiro tem considerado a possibilidade de repavimentar a BR-319, trazendo à tona grandes discussões sobre os possíveis

impactos à biodiversidade que a reabertura da estrada pode causar (Fearnside 2006; Fearnside & Graça 2006).

Projeções dos impactos da reativação da rodovia indicam que o desmatamento ocupará uma grande quantidade de nascentes dos riachos do interflúvio Purus-Madeira (Fearnside 2006; Fearnside & Graça 2006; Maldonado *et al.* 2009). A retirada da mata, a agricultura mecanizada e a pecuária aumentarão a perda dos solos e proporcionarão a colmatção de diversos igarapés, degradando gravemente o ambiente aquático e sua fauna associada (Fearnside 2006; Fearnside & Graça 2006). Compreender como a ictiofauna pode ser afetada por estas intervenções é uma tarefa que exige um arcabouço de informações seguras sobre a composição e a dinâmica das assembleias. O estudo do impacto ambiental da repavimentação da BR 319 contemplou apenas 14 corpos d'água para todo o interflúvio, sendo apenas cinco referentes a igarapés, com as coletas limitadas aos riachos que cruzam a rodovia, sem abordar escalas temporais (IBAMA 2009). Essa amostragem não permite uma análise robusta dos processos ecossistêmicos que atuam sobre os padrões de diversidade de peixes de riacho da região.

Trabalhos sobre taxonomia ainda são necessários para os peixes de riachos amazônicos, considerando que muitos táxons são mal resolvidos ou incluem espécies de difícil identificação, com amplas diferenças morfológicas e genéticas e complexos de espécies crípticas (Mendonça 2010). Ter informações de alta qualidade sobre a composição taxonômica das espécies que ocorrem em determinada região é uma das principais premissas para a implementação de programas efetivos de monitoramento biológico (Rapp Py-Daniel *et al.* 2007), sobretudo em áreas que estão sujeitas à fortes impactos antrópicos. Em primeiro lugar, é necessário ampliar o nível de conhecimento das espécies que ocorrem no interflúvio Purus-Madeira, contemplando as drenagens da região central do interflúvio e resolver as indefinições taxonômicas ainda existentes. Assim, no **primeiro capítulo** desta tese nós apresentamos uma lista de ocorrência dos peixes de riacho do interflúvio Purus-Madeira, construída a partir de novas expedições científicas às drenagens de difícil acesso da porção central do interflúvio e

que também incorpora os registros previamente listados para a região, atualizados e corrigidos de acordo com a literatura científica mais recente.

Um segundo passo importante é compreender como as características da paisagem e as condições locais determinam o padrão de distribuição destas espécies ao longo do interflúvio. Em assembleias de peixes de riacho, é sabido que as características do ambiente e a disponibilidade de habitat filtram as espécies localmente de acordo a capacidade específica de explorar e competir por recursos (Medonça *et al.* 2005, Terra *et al.* 2015, Arantes *et al.* 2017, Benone *et al.* 2017) enquanto que a limitação de dispersão e os fatores históricos atuam em amplas escalas determinando o *pool* regional de espécies (Cilléros *et al.* 2016; Albert *et al.* 2011; Peláez & Pavanelli, 2018). No entanto, os efeitos dos processos locais e regionais sobre as assembleias podem ser limitados ou amplificados pela configuração espacial da drenagem, que determina a permeabilidade e a dinâmica de fluxo de indivíduos entre habitats (Nekola *et al.* 1999; Brown & Swan 2010; Altermatt & Fronhofer 2017).

A posição do riacho com relação aos grandes rios aumenta as possibilidades de dispersão entre habitats e o papel de “efeitos de massa” e de “fonte-sumidouro” nos padrões de estruturação local (Gorman 1989; Osorne & Wiley 1992, Schlosser 1991). A proximidade com a planície de inundação também pode favorecer espécies que utilizam os ambientes alagados durante a cheia para alimentação ou desova, o que diminui processos de competição e potencializa o recrutamento das populações que habitam essa interface (Espírito-Santo *et al.* 2013; Couto *et al.* 2017). Nesse sentido, riachos de tamanho semelhante podem alocar número de espécies e de indivíduos bastante variável de acordo com a sua posição dentro da rede de drenagem e sua conectividade com grandes bacias, mas esta variável tem sido pouco considerada em estudos na Amazônia.

Em assembleias tropicais onde a alta riqueza e a heterogeneidade de habitats geram padrões complexos de respostas, uma análise conjunta da variação taxonômica e funcional pode fornecer uma compreensão mais clara dos gradientes que estão determinando as mudanças entre habitats (Mason *et al.* 2005). Quando os efeitos de fatores estocásticos ou históricos predominam na estruturação das

assembleias em detrimento das características locais, é esperado que as assembleias variem taxonomicamente devido a processos de deriva, mas exibam composição funcional semelhante, já que a disponibilidade de recurso localmente é semelhante entre habitats (Cilléros *et al.* 2016, Terra *et al.* 2016). Em contrapartida, se há mudanças na disponibilidade de recursos ou filtros espaciais que limitam ou facilitam a chegada de determinadas espécies entre trechos da paisagem, a variação taxonômica deve ser acompanhada por mudanças nas estratégias funcionais, já que as assembleias poderão divergir na forma de explorar os recursos (Swenson *et al.* 2011, Villéger *et al.* 2008). **No segundo capítulo** desta tese nós buscamos compreender como a composição taxonômica e funcional das assembleias de peixes de riacho do interflúvio Purus-Madeira estão sendo filtradas por variáveis locais e da paisagem e avaliar o efeito da proximidade com os grandes rios na determinação destes padrões.

Abordagens que envolvam escalas temporais também são fundamentais para determinar quantas mensurações são necessárias para descrever adequadamente as assembleias e quais os processos chaves que atuam na estruturação das mesmas. Se não existem grandes mudanças sazonais, monitoramentos da ictiofauna podem ser feitos em qualquer período do ano, mas se existirem mudanças significativas, monitoramentos deveriam ser padronizados em relação às mudanças sazonais, ou as mudanças sazonais serem consideradas *a priori* nas análises, isolando seus efeitos sobre as demais variáveis (Espírito-Santo 2005). Os riachos que compõe a rede de drenagem do interflúvio Purus-Madeira apresentam fluxo de vazão bastante sincronizado ao da planície de inundação circundante, e durante os períodos de água baixas grande parte dos pequenos corpos d'água secam completamente ou são reduzidos a poças desconectadas que permanecem no leito dos igarapés. Apesar de riachos intermitentes serem bastante frequentes ao redor do mundo (Tooth 2000; Sheldon *et al.*, 2010, Larned *et al.*, 2010), a ocorrência de intermitência em riachos de florestas ombrófilas é pouco conhecida (Datry *et al.*, 2016), assim como o entendimento sobre sua fauna associada. **No terceiro capítulo** nós analisamos as variações interanuais de composição das assembleias de peixes de 11 riachos intermitentes do interflúvio Purus-Madeira, e o

papel das variações das condições do habitat e da conectividade com a planície de inundação na estabilidade e persistência das espécies.

OBJETIVOS

1º capítulo

- Realizar amostragens nas diversas sub-bacias que compõe o interflúvio Purus-Madeira e aumentar o conhecimento sobre a fauna de peixes de diferentes porções do interflúvio;
- Compilar os registros de ocorrência realizados anteriormente para a região e criar uma lista atualizada sobre a fauna de peixes do interflúvio Purus-Madeira, que sirva de subsídio para novos estudos;

2º capítulo

- Determinar os padrões de distribuição das espécies ao longo dos gradientes espaciais do interflúvio Purus-Madeira;
- Determinar os efeitos da distância ao grande rio, da distância por água e das variáveis locais sobre os padrões de dissimilaridade funcional e taxonômica da ictiofauna da região;

3º capítulo

- Caracterizar a variabilidade interanual das assembleias de peixes de riachos intermitentes do interflúvio Purus-Madeira;
- Determinar os efeitos das variáveis locais e da conectividade com a planície de inundação sobre a estabilidade interanual da composição das assembleias de peixes de riacho;

ARTIGO 1

Updated checklist of headwater stream fishes of the Purus-Madeira interfluve, Central Amazonia

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Manuscrito em revisão na *Acta Amazonica*

Abstract

The Purus-Madeira interfluvium constitutes a high biodiversity area whose stream-fish fauna remains scarcely known. The few available information remains limited to small drainages close to major urban centers and to large rivers. This study aims to increase the knowledge about the stream-fish assemblages of the Purus-Madeira interfluvium and to provide a comprehensive and up-to-date species list, integrating studies previously developed in the region. We sampled 39 stream reaches distributed in 10 catchments over a stretch of 700 km along the main axis of the BR-319 highway that cross the Amazonas state, between 2014 and 2017. For the checklist creation, we merged our occurrence records with those previously listed for the region, updating the identifications of some species when necessary. We collected 12,566 specimens belonging to 113 species distributed in 20 families and seven orders. Characiformes harbored the largest number of species (64 species), followed by Siluriformes (17) and Gymnotiformes (11). Characiformes was also the most abundant order, with 9,822 specimens, and five species (*Hemigrammus bellottii*, *Hyphessobrycon* cf. *wosiackii*, *Copella callolepis*, *Hemigrammus ocellifer* and *Hemigrammus melanochromis*) accounted for 54% of the collected fish. The combination of our occurrence records with those from literature resulted in a list of 184 species, of which 43 were exclusively present in our samples. Our results show that Purus-Madeira interfluvium hosts a high diversity of stream fishes and highlight the importance of further studies in the region, since repaving plans of BR-319 highway can significantly impact headwater systems and suppress key areas for maintaining fish diversity.

Keywords: Ichthyofaunal diversity; Freshwater inventory; Neotropical fauna; Amazon basin, Road impacts.

Lista atualizada das espécies de peixes de riacho do interflúvio Purus-Madeira, Amazônia

Central

Resumo

O interflúvio Purus-Madeira é uma região conhecida pela alta biodiversidade, cuja fauna de peixes de riacho permanece pouco conhecida. As poucas informações disponíveis estão limitadas as drenagens próximas aos centros urbanos ou aos grandes rios. Esse estudo objetiva ampliar o conhecimento sobre os peixes de riacho do interflúvio Purus-Madeira e fornecer uma lista de espécies atualizada e abrangente, integrando estudos previamente desenvolvidos na região. Foram amostrados 39 riachos distribuídos em 10 drenagens ao longo de 700 km da rodovia BR-319, no estado do Amazonas, entre os anos de 2014 e 2017. Para a criação da lista de espécies, nós combinamos nossos registros de ocorrência com aqueles previamente listados para a região, atualizando o status taxonômico das espécies quando necessário. Foram coletados 12,566 espécimes pertencentes a 113 espécies, distribuídos em 20 famílias e sete ordens. Characiformes apresentou a maior diversidade (64 espécies), seguida de Siluriformes (17) e Gymnotiformes (11). Characiformes também foi a ordem mais abundante, com 9,822 espécimes, e cinco espécies juntas (*Hemigrammus bellottii*, *Hyphessobrycon* cf. *wosiackii*, *Copella collolepis*, *Hemigrammus ocellifer* and *Hemigrammus melanochrous*) somaram 54% do total coletado. A combinação dos nossos registros de ocorrência com aqueles da literatura resultaram em uma lista de 184 espécies, das quais 43 foram apenas coletadas na nossa amostragem. Nossos resultados mostram que o interflúvio Purus-Madeira abriga uma alta diversidade de peixes e ressaltam a importância da continuidade de estudos na região, uma vez que a repavimentação da BR-319 deve gerar impactos significativos nos ambientes de cabeceira e suprimir áreas fundamentais para a manutenção da biodiversidade.

Palavras chave: Diversidade ictiofaunística; Ecologia de água doce, Fauna neotropical; Bacia Amazônica, Impacto de estradas.

Introduction

The Purus-Madeira interfluve represents a large forested area approximately 800 km long that contains high biodiversity and endemism areas of different taxonomic groups (Cohn-Haft *et al.* 2007; Rohe *et al.* 2007; Buhrnheim *et al.* 2008; Barros *et al.* 2011). The presence of different vegetation types, such as “terra-firme” forests, “campinaranas” and flooded forests, results in habitat heterogeneity that regulates complex diversification processes that only been very recently assessed (Ferrão *et al.* 2016; Ferreira *et al.* 2018; Ortiz *et al.* 2018). This high diversity is also expected for the small streams that drain the interfluve, which forms a dense network with peculiar hydrological dynamics associated with seasonally flooded paleo-floodplains and intermittent streams with rain-dependent hydroperiods (Cintra *et al.* 2013). In spite of many expeditions carried out in the last decades that have focused on the fish fauna of the Madeira River and its main tributaries (Goulding 1980; Rapp Py-Daniel *et al.* 2007; Queiroz *et al.* 2013; Vieira *et al.* 2016), the knowledge about the species that inhabit the headwaters of small drainages farthest from the large rivers is still scarce, mostly resulting from accessibility difficulties.

Barros *et al.* (2011) investigated the ichthyofauna of 22 streams in sub-basins near Manaus and Humaitá and found 78 species, a higher value than other studies that analyzed a larger number of streams in other locations in Amazonia (Araújo-Lima *et al.* 1999; Bührnheim and Cox-Fernandes 2003; Mendonça *et al.* 2005; Espírito-Santo *et al.* 2009). Vieira *et al.* (2016) investigated eight streams of Cuniã drainage, an affluent of Madeira river, and found 141 species within an area of 25 km², which represents twice the number of species recorded for the entire Ducke, a 100 km² forest area near of Manaus, whose ichthyofauna was widely studied in recent years (Zuanon *et al.* 2015). It is worth noting that 19% of the species found by Barros *et al.* (2011) and 26% of those found by Vieira *et al.* (2016) did not have fully defined taxonomic status, indicating the lack of robust information about the fish diversity of these systems. Sampling insufficiency is more evident in remote drainages, distant from

large urban centers and from large rivers, which are the closest and most vulnerable to the imminent impacts of repaving the BR 319 highway. The highway runs through the entire interfluve and projections of impacts indicate that a large number of headwaters systems will be deforested, substantially compromising the integrity of these environments (Fearnside 2006; Maldonado *et al.* 2009). Environmental-impact studies of the BR 319 highway sampled only 14 water bodies and samples were limited to the aquatic environments that cross the highway (IBAMA 2009). This information is sufficient to form the basis of biological monitoring programs or to accurately predict the impacts of road reactivation in such a complex net of streams.

Understanding how anthropic impacts can change fish assemblage structure requires secure information about the composition and distribution patterns of species in the landscape. This study aims to increase the knowledge about the stream-fish diversity of the Purus-Madeira interfluve and the composition patterns of fish assemblages in different portions of the drainage. We also provide a comprehensive and up-to-date species list for the area, integrating previous studies undertaken in the Purus-Madeira interfluve, to guide future ecological studies and appropriate management plans.

Materials and Methods

Study area

Sampling was undertaken along 700 km of the Madeira-Purus interfluve, in southwestern Amazonas state, Brazil. The region (Fig 1) is covered by dense rainforest with mean annual precipitation varying from 2000 to 2400 mm (Sombroek 2000). The interfluve is inserted in the Içá Formation of Plio-Pleistocene deposits, which represent the uppermost sedimentary deposits of the current lowland “terra firme” forest substrates in Central Amazonia (Pupim *et al.* 2019). Predominant soil texture in the region is silt to fine sand and relief varies from flat to gently undulating, which results in poorly drained soils (Sombroek 2000). The combination of flat relief and the high annual flood pulses of the Purus, Madeira and Amazon Rivers, which usually exceed 10 m (Junk *et al.* 1989), creates marginal lakes and temporarily-inundated systems during the wet season. However, the

shallow water table does not sustain surface flow in headwaters through consecutive drought months after the rain stops, causing part of the smaller streams to dry completely for months, or persisting as isolated pools along the stream-bed. This hydrological fluctuation determines a highly dynamic landscape, especially in headwater systems, which experience drought and flood conditions within short periods of time (Stegmann *et al.* 2019).

Fish sampling

We sampled 39 headwater-stream reaches (50 m long reaches in 1st to 3rd order streams) in 10 catchments along the Madeira-Purus interfluvium that drain to the Madeira or Amazon Rivers (coordinates in Table 1). Stream reaches from catchments 5, 6, 7, 8, 9 and 10 were sampled only once, during expeditions conducted between December 2014 and March 2015. In order to have more information about seasonal changes in the assemblages composition, catchments 1, 2, 3 and 4, with easier access due to better road conditions, were sampled five times over 3 years (November 2015, March 2016, October 2016, May 2017 and December 2017).

In each stream, a 50 m long reach was isolated with block nets (5mm mesh) and fish were caught using seine and hand nets. Fish were collected only during the day and collection effort in each section was standardized by using two collectors over two hours. The specimens were euthanized in Eugenol solution, which decreases fish neurosensory functions by acting upon the nervous systems. The specimens were later fixed in 10% formalin and preserved in 70% ethanol. Fishes were sorted, counted and identified to species level in the laboratory using dichotomous keys and specialized literature, such as Géry (1977), Buckup (1993), Queiroz *et al.* (2013) and Zuanon *et al.* (2015), as well as by comparison to specimens deposited at the Fish Collection of the National Institute for Research in the Amazon (INPA, Manaus, Amazonas state, Brazil). Voucher specimens of all collected species were sent to INPA's fish collection.

Checklist update

For the checklist creation, we merged our occurrence records with those previously listed by Barros *et al.* (2011) and Vieira *et al.* (2016), the only published studies about the fish fauna of that region we have notice. In order to avoid possible record duplications, we have only considered as valid species those that were identified to species level by the mentioned authors. We also considered species identified only to genus level when it represented the only record for that genus in the study area.

The identification of seven species was updated or rectified, after analysis of the previously deposited material. Specimens previously identified as *Hyphessobrycon heterorhabdus* by Barros *et al.* (2011) are now reidentified as *Hyphessobrycon* cf. *wosiackii*. Similarly, specimens previously identified as *Copella nattereri* were reidentified as *Copella callolepis*, as were those identified as *C. nigrofasciata* (a junior synonym of *C. callolepis*). Specimens of *Pyrrhulina brevis* have now been identified as *Pyrrhulina laeta*, due to updates in genus classification. *Gymnorhamphichthys petiti* was considered a junior synonym of *G. rondoni* and specimens of *Sternopygus aequilabiatus* were reidentified as *S. macrurus*. The specie *Trichomycterus hasemani* has been updated to *Potamoglanis hasemani*. Finally, specimens reidentified as *Moekhausia* cf. *diktoya* by Barros *et al.* (2011) were reanalyzed and identified as *Hemigrammus pretoensis*.

Results

Ichthyofaunal composition

We collected 12,566 specimens belonging to 113 species distributed in 20 families and seven orders (Table 2). Characiformes had the largest number of species (64), followed by Siluriformes (17) and Gymnotiformes (11). Cyprinodontiformes and Cichliformes presented eight and nine species, respectively, and Synbranchiformes and Beloniformes had two species each (Figure 2). Characiformes was also the most abundant order, with 9,822 specimens, representing 78% of the total captured. Cichliformes was the second most abundant order, with 1,249 specimens, followed by Siluriformes with 782 specimens. Gymnotiformes and Cyprinodontiformes were 4th and 5th in abundance, with 435 and 222 specimens respectively. The family with the largest number of species was Characidae (62),

followed by Cichlidae (18). Crenuchidae and Loricariidae had 12 species each and Lebiasinidae was 5th with 11 species.

Five species (*Hemigrammus bellottii*, *H. cf. wosiackii*, *Copella callolepis*, *H. ocellifer* and *H. melanochrous* in decreasing order of contribution) accounted for 54% of the total number of captured individuals. Although less abundant, *Apistogramma agassizii*, *Carnegiella strigata*, *Crenuchus spilurus* and *Hoplias malabaricus* were widely distributed, occurring in at least eight of the 10 catchments analyzed. Thirty eight species were captured only once and catchments 1, 3 and 6 had the largest number of exclusive species (15, 13 and six, respectively).

The catchments with the largest sampling effort (1 to 4) had the largest number of species collected, and the catchment 3 has the largest number (65) of species recorded. Even though catchment 9 was sampled only once, we captured as many species (38) there as in most catchments sampled over three years and it had the highest average number of species per stream reach (19 species). Catchment 7 had the lowest number of species (17 species) and also the least number of individuals (185) and the lowest average number (6) of species per stream reach.

Updated checklist

The combination of our occurrence records with those previously recorded for the Purus-Madeira interfluvium resulted in a list of 184 species, 27 families and eight orders. Thirty five species were collected in the three studies and 43 species were captured exclusively in our samples, of which 19 were species of Characiformes, nine were Siluriformes, five were Gymnotiformes, five were Cyprinodontiformes, three were Cichliformes and two were Beloniformes (Figure 3). Twelve species, mostly Characidae, were recorded only by Barros *et al.* (2011). Vieira *et al.* (2016) had the highest number of exclusive records (50 species) mainly from Characiformes (23 species), Siluriformes (17 species) and Cichliformes (7 species).

Discussion

The new occurrence records from our study highlights the high diversity of stream fishes occurring in the catchments of the Purus-Madeira interfluve and how limited is our knowledge of these systems. The genera *Leptobrycon*, *Copeina*, *Tridentopsis*, *Rhamdella* and *Moema* had not previously been recorded for the Madeira River basin, which is one of the best-studied drainages in the Brazilian Amazon. In part, this is due to the concentration of previous sampling efforts around the main channel of the Madeira River or in direct tributaries, while headwater systems in more isolated areas were less investigated and have distinct taxonomic groups. In addition, the diversity of vegetation types in the Purus-Madeira interfluve, with presence of both paleo-floodplain and open forests, favors the establishment of species with variable ecological demands, even over short spatial scales. In this sense, spatially-standardized inventories such the one conducted by us are more efficient in providing comprehensive data about the biodiversity of the region.

The high fish species richness found in some catchments may be related to the fact that these streams are located in lowland riverine terraces, which are subject to frequent flooding that can reach up to 5 m, influenced by the flood pulse of large rivers (Moulatlet *et al.* 2014). These fluctuations in water level provide opportunities for semi-isolated communities in headwater streams to come in contact during flooding periods (Lowe-McConnell 1975; Albert *et al.* 2011), which may increase colonization events and species interchange, resulting in species accumulation in these areas. Future studies using genomic approaches are needed to identify if these region is acting as an “evolutionary museum”, a region of net species accumulation where rates of extinction are lower than the combined rates of speciation and immigration (Stenseth 1984; Albert *et al.* 2011).

Some catchments analyzed over three years had twice the number of species as those sampled only once, although the sample protocol used was identical in all sites. This results reinforces the need for long term studies to mitigate detection failures and to better understand mechanisms operating on species substitution over time. Central Amazon fish assemblages are considered relatively stable between seasons in perennial upland streams (Buhrnheim and Cox Fernandes 2001; Espirito-Santo *et*

al. 2009), the peculiar hydrological dynamics of headwater systems in Purus-Madeira interfluvium cause strong temporal variation in species distribution. This occurs because stream fishes are forced to migrate following the water level and are constantly recolonizing the newly flooded environments. Despite the high values of species richness found per catchment, the average number of species per stream reach was not much higher than that found in other studies carried out in Amazonian streams (e.g. Mendonça *et al.* 2005). This result is in line with that found by Stegmann *et al.* (2019) who detected a high species turnover along the Purus-Madeira interfluvium, even between geographically close catchments.

The dominance of Characidae is in agreement with other studies carried out in Amazonian streams (Sabino and Zuanon 1998; Araújo-Lima *et al.* 1999; Mendonça *et al.* 2005) and reflects the high morphological diversification of the family, with species able to explore different types of resources and habitat types (Reis *et al.* 2003; Queiroz *et al.* 2013) in a restricted environment as a small stream. Siluriformes was the second order in number of species, but this pattern was not homogeneous for all sites analyzed, as Gymnotiformes had a greater number of species in catchments 2, 4 and 5, which is unusual for Neotropical streams. This was also observed by Barros *et al.* (2011) who found a higher number of species and individuals of Gymnotiformes than of Siluriformes. The flat topography of the region favors accumulation of leaf litter in stream beds, which is the preferred habitat of many species of those electric fishes (especially of Hypopomidae and Gymnotidae) and may favor the recruitment of these populations and diversification processes. The flat topography also causes most of the streams to have very slow flow velocity, which may favor miniaturized species, such as those from the genera *Odontocharacidum*, *Amazonspinther*, *Axelrodia*, *Priocharax*, *Tytocharax* and *Microphilypnus*. These frequently captured species generally have little swimming capacity and low resistance to strong flows (Weitzman and Vari 1988), so are seldom found in streams with high current velocity running across steep topographies.

To have accurate information on the species composition of a region is paramount for effective monitoring plans and for the proper ecosystems conservation (Rapp Py-Daniel *et al.* 2007; Magnusson *et al.* 2013). Therefore efforts to catalogue and better assess biodiversity need to be prioritized (Bickford *et al.* 2006). Despite our effort to resolve possible taxonomic uncertainties, the number of species that need taxonomic confirmation in our final list is still high (34 species), which makes clear the importance of further studies in the region. In addition, species with large areas of occurrence, such as *Apistogramma agassizii*, *Copella collolepis* and *Hemigrammus bellottii*, may represent species complexes and need to be better studied with techniques that integrate morphological and molecular data (Ferrão *et al.* 2016).

The number of species that we have listed for the streams of Purus-Madeira interfluve is more than twice that indicated in the environmental-impact study for the BR-319 highway repaving (IBAMA, 2009). In addition, that study focused only on large water bodies that cross the highway, whereas headwater systems were not studied, despite being highly vulnerable environments to changes in the riparian and catchment's vegetation (Leitão *et al.* 2017) and system fragmentation (Perkin and Hard 2012). The loss of vegetation can quickly change the nature of the streams substrates and increase water temperature, leading to local extinctions and the loss of important ecological functions (Leitão *et al.* 2018). None of the fish species recorded for the streams of the Purus-Madeira interfluve are currently considered threatened by extinction (ICMBIO 2018); however, some species so far recorded only for that area may be endangered by the impacts of the reactivation of the BR-319 highway, such as the iconic *Amazonspinther dalmata*, which is only known for the Purus-Madeira interfluve (Bührnheim *et al.* 2008). The maintenance of ecosystem services for the entire drainage basin can only be guaranteed if the species that inhabit the headwater systems are considered both in the highway-impact studies and in future mitigation plans.

Conclusion

Our study is the first to provide a compiled list of stream-fish species covering several catchments over a 700 km stretch in Purus-Madeira interfluve. The number of species recorded is higher than those usually found in other amazonian studies in streams systems and suggests that Purus-Madeira interfluve houses a biodiversity whose structuring factors still need to be better understood. This information should be considered in impact studies of the BR-319 highway and should guide the delimitation of priority areas for conservation plans.

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TABLES

Table 1. Geographical coordinates and habitat characterization of 39 stream reaches sampled in the Purus-Madeira interfluve.

	Site code	Geographical coordinates		Mean width (cm)	pH
1	M01_1	-3,3527726	-59,8534254	309,67	4,39
	M01_2	-3,3490044	-59,8384719	93,67	3,83
	M01_3	-3,3450518	-59,8223516	364,67	4,28
	M01_4	-3,3632317	-59,8581639	532,67	4,26
2	M02_1	-3,6877721	-60,331698	216,67	4,40
	M02_2	-3,6715119	-60,3055174	253,33	4,28
	M02_3	-3,6697975	-60,3024815	252,33	4,45
3	M03_1	-4,1336734	-60,7358268	120,33	4,26
	M03_2	-4,1351736	-60,7343743	173,33	4,30
	M03_3	-4,1460881	-60,727338	427,33	4,53
	M03_4	-4,1500646	-60,7261475	175,67	4,06
	M03_5	-4,1598451	-60,7242068	181,33	4,49
4	M04_1	-4,3794509	-60,9480321	132,67	3,96
	M04_2	-4,3835941	-60,9434365	232,67	4,04
	M04_3	-4,3998714	-60,9269234	264,00	3,61
	M04_4	-4,4029609	-60,9245214	181,33	3,58
5	M05_1	-4,6151031	-61,2444469	311,67	4,38
	M05_2	-4,6054573	-61,2543983	196,67	4,54
	M05_3	-4,6083749	-61,2511888	131,00	4,00
	M05_4	-4,6013743	-61,2610096	129,00	4,40
	M05_5	-4,588043	-61,2781114	136,67	4,32
6	M06_1	-4,9937038	-61,5731835	400,00	4,08
	M06_2	-4,9958111	-61,5710048	446,67	4,32
	M06_3	-4,9912037	-61,5783625	496,67	3,84
	M06_4	-5,0030617	-61,5616112	460,00	4,73
7	M07_1	-5,2669524	-61,9331671	130,00	4,44
	M07_2	-5,2632378	-61,9371317	306,67	4,38
	M07_3	-5,252874	-61,9459181	386,67	4,20
	M07_4	-5,2419847	-61,9578654	356,67	4,10
8	M08_1	-5,6284677	-62,1965617	600,00	4,56
	M08_2	-5,6328877	-62,1862752	121,67	4,45
	M08_3	-5,6383524	-62,179605	436,00	4,33
	M08_4	-5,6450225	-62,166988	536,67	3,97
9	M9_1	-7,2058707	-63,120927	432,00	3,80
	M9_2	-7,2099692	-63,1127299	168,33	3,71
	M9_3	-7,2128623	-63,1053767	224,67	2,80
10	M10_1	-7,56524412	-63,11569292	174,32	3,58
	M10_2	-7,56530581	-63,11401729	124,2	3,91
	M10_3	-7,56579783	-63,1129035	134,78	3,7

Table 2. Checklist of stream-fish species recorded in the Purus-Madeira interfluve. The list contains the occurrence records from our study and those previously recorded by Barros *et al* (2011) and Viera *et al.* (2016). Numbers indicate the abundance of each species in our samples. Asterisks indicate species that were not recorded in our samplings.

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
Myliobatiformes													
Potamotrygonidae													
<i>Potamotrygon</i> sp.	*	*	*	*	*	*	*	*	*	*	*		X
Characiformes													
Curimatidae													
<i>Curimatopsis crypticus</i> Vari, 1982			66								66		X
<i>Curimatopsis macrolepis</i> (Steindachner, 1876)			5								5		X
<i>Cyphocharax pantostictos</i> Vari & Barriga, 1990	*	*	*	*	*	*	*	*	*	*	*	X	
Anostomidae													
<i>Pseudanos gracilis</i> (Kner, 1858)	*	*	*	*	*	*	*	*	*	*	*		X
Crenuchidae													
<i>Ammocryptocharax elegans</i> (Weitzman & Kanazawa, 1976)						5					5		X
<i>Characidium</i> aff. <i>etheostoma</i> Cope, 1872	*	*	*	*	*	*	*	*	*	*	*		X
<i>Characidium</i> cf. <i>pellucidum</i> Eigenmann, 1909	*	*	*	*	*	*	*	*	*	*	*		X
<i>Characidium</i> cf. <i>pterooides</i> Eigenmann, 1909	*	*	*	*	*	*	*	*	*	*	*		X
<i>Crenuchus spilurus</i> Günther, 1863	33	175	89	78	8	2	5	4	1		395	X	X
<i>Elachocharax junki</i> (Géry, 1971)	*	*	*	*	*	*	*	*	*	*	*	X	X
<i>Elachocharax pulcher</i> Myers, 1927			16			4	1				21	X	X
<i>Melanocharacidium dispilomma</i> Backup, 1993	*	*	*	*	*	*	*	*	*	*	*		X
<i>Microcharacidium eleotrioides</i> (Géry, 1960)								3	1		4		X
<i>Microcharacidium gnomus</i> Backup, 1993		2	5	61	1						69		X
<i>Microcharacidium weitzmani</i> Backup, 1993			4		8	7		5			24	X	
<i>Odontocharacidium aphanes</i> (Weitzman & Kanazawa, 1977)			14		2			7	2		25	X	X
Gasteropelecidae													

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Carnegiella marthae</i> Myers, 1927			2								2	X	X
<i>Carnegiella strigata</i> (Günther, 1864)	37	18	92	43	19		2		4	6	221	X	X
<i>Gasteropelecus sternicla</i> (Linnaeus, 1758)	80										80		
Characidae													
<i>Amazonspinther dalmata</i> Bührnheim, Carvalho, Malabarba & Weitzman, 2008					2	1	1		11		15	X	X
<i>Astyanax</i> aff. <i>bimaculatus</i> (Linnaeus, 1758)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Axelrodia lindeae</i> Géry, 1973	*	*	*	*	*	*	*	*	*	*	*		X
<i>Axelrodia stigmatias</i> (Fowler, 1913)			29			1		14		3	47		X
<i>Aphyocharacidium bolivianum</i> Géry, 1973	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Bario steindachneri</i> (Eigenmann, 1893)			2								2	X	X
<i>Bryconella pallidifrons</i> (Fowler, 1946)			27						55	20	102		X
<i>Bryconops</i> aff. <i>magoi</i> Chernoff & Machado-Allison, 2005	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Bryconops</i> aff. <i>alburnoides</i> Kner, 1858	*	*	*	*	*	*	*	*	*	*	*		X
<i>Bryconops</i> cf. <i>caudomaculatus</i> (Günther, 1864)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Bryconops</i> cf. <i>giacopinii</i> (Fernández-Yépez, 1950)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Bryconops inpai</i> Knöppel, Junk & Géry, 1968	*	*	*	*	*	*	*	*	*	*	*		X
<i>Charax caudimaculatus</i> (Lucena, 1987)	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Chrysobrycon hesperus</i> (Böhlke, 1958)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Gnathocharax steindachneri</i> Fowler, 1913			20						22	1	43	X	X
<i>Gymnocorymbus thayeri</i> Eigenmann, 1908	8										8		
<i>Hemigrammus bellottii</i> (Steindachner, 1882)	192	43	1900		20	152		4	24	303	2638	X	X

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Hemigrammus cf. analis</i> Durbin, 1909	*	*	*	*	*	*	*	*	*	*	*	X	X
<i>Hemigrammus geisleri</i> Zarske & Géry, 2007										17	17		X
<i>Hemigrammus gracilis</i> (Lütken, 1875)	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Hemigrammus cf. hyanuary</i> Durbin, 1918						1			6		7		
<i>Hemigrammus levis</i> Durbin 1908	*	*	*	*	*	*	*	*	*	*	*		X
<i>Hemigrammus lunatus</i> Durbin 1918	*	*	*	*	*	*	*	*	*	*	*		X
<i>Hemigrammus melanochrous</i> Fowler, 1913		189	49	167	171	18	134	50	55		833		X
<i>Hemigrammus ocellifer</i> (Steindachner, 1882)	466	4	337			1			50	85	943	X	X
<i>Hemigrammus vorderwinkleri</i> Géry, 1963			237							15	252	X	X
<i>Hemigrammus pretoensis</i> Géry, 1965			3		3						6	X	
<i>Hemigrammus schmardae</i> (Steindachner, 1882)	2										2	X	
<i>Hemigrammus unilineatus</i> (Gill, 1858)	181										181		
<i>Hoplocharax goethei</i> Géry, 1966			3								3		
<i>Hyphessobrycon agulha</i> Fowler, 1913				7	3	4	3		2		19		X
<i>Hyphessobrycon bentosi</i> Durbin, 1908			2							2	4		X
<i>Hyphessobrycon copelandi</i> Durbin, 1908			18								18		
<i>Hyphessobrycon cf. tukunai</i> Géry, 1965	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Hyphessobrycon cf. wosiackii</i> Moreira & Lima, 2017		330	130	251	120		1	12	482		1326	X	
<i>Hyphessobrycon eques</i> Steindachner, 1882	*	*	*	*	*	*	*	*	*	*	*		X
<i>Hyphessobrycon sweglesi</i> (Géry, 1961)									3	6	9		X
<i>Iguanodectes cf. spilurus</i> (Günther, 1864)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Iguanodectes geisleri</i> Géry, 1970				1		3	4	9			17	X	X
<i>Iguanodectes purusi</i> (Steindachner, 1908)	1			10	1		4	1		1	18		X
<i>Iguanodectes variatus</i> Géry, 1993	*	*	*	*	*	*	*	*	*	*	*	X	X
<i>Microschemobrycon casiquiare</i> Böhlke, 1953						3					3		
<i>Jupiaba anteroides</i> (Géry, 1965)	*	*	*	*	*	*	*	*	*	*	*		X

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Microchemobrycon geisleri</i> Géry, 1973	*	*	*	*	*	*	*	*	*	*	*		X
<i>Microchemobrycon guaporensis</i> Eigenmann, 1915	*	*	*	*	*	*	*	*	*	*	*		X
<i>Moenkhausia aff. naponis</i> Böhlke, 1958	15									2	17		
<i>Moenkhausia comma</i> Eigenmann, 1908	26										26		
<i>Moenkhausia chrysargyrea</i> (Günther, 1864)	15		2								17	X	X
<i>Moenkhausia collettii</i> (Steindachner, 1882)										7	7	X	X
<i>Moenkhausia cotinho</i> Eigenmann, 1908	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Moenkhausia intermedia</i> Eigenmann, 1908	*	*	*	*	*	*	*	*	*	*	*		X
<i>Moenkhausia lepidura</i> (Kner, 1858)								1			1		
<i>Moenkhausia mikia</i> Marinho & Langeani, 2010			1			1					2	X	X
<i>Moenkhausia oligolepis</i> (Günther, 1864)	3	2							1		6	X	X
<i>Oxybrycon parvulus</i> Géry, 1964			23	6					1		30		
<i>Phenacogaster cf. beni</i> Eigenmann, 1911	*	*	*	*	*	*	*	*	*	*	*		X
<i>Phenacogaster cf. pectinatus</i> (Cope, 187)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Phenacogaster cf. retropinnus</i> Lucena & Malabarba, 2010	7										7		
<i>Priocharax ariel</i> Weitzman & Vari, 1987			233					21			254	X	X
<i>Leptobrycon</i> sp.										2	2		
<i>Tyttocharax madeirae</i> Fowler, 1913			3			7		29			39	X	X
<i>Xenrobrycon polyancistrus</i> Weitzman, 1987						8					8		X
Acestrorhynchidae													
<i>Acestrorhynchus falcatus</i> (Bloch, 1794)		1	1	6							8		X
Erythrinidae													
<i>Erythrinus erythrinus</i> (Bloch & Schneider, 1801)	16	106	23	59	1				9		214	X	X
<i>Hoplerythrinus unitaeniatus</i> (Agassiz, in Spix & Agassiz, 1829)	10	12		1							23	X	X

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Hoplias malabaricus</i> (Bloch, 1794)	40	50	25	15	1			1	1	2	135	X	X
Lebiasinidae													
<i>Copeina guttata</i> (Steindachner, 1876)	154										154		
<i>Copella callolepis</i> (Steindachner, 1876)	264	65	559	11	42	4	3	10	17	3	978	X	X
<i>Nannostomus unifasciatus</i> Steindachner, 1876			2								2		
<i>Nannostomus digrammus</i> Fowler, 1913			31								31		X
<i>Nannostomus marginatus</i> (Eigenmann, 1909)		2									2		
<i>Nannostomus eques</i> Steindachner, 1876	26		21							9	56	X	X
<i>Nannostomus trifasciatus</i> Steindachner, 1876	1	14							10		25		
<i>Pyrrhulina laeta</i> (Cope, 1872)	69	25	75	73	16		8		7		273	X	X
<i>Pyrrhulina semifasciata</i> Steindachner, 1876	43		10								53		
<i>Pyrrhulina zigzag</i> Zarske & Géry, 1997	11										11	X	
<i>Pyrrhulina lugubris</i> Eigenmann, 1922	7		2								9		
Siluriformes													
Auchenipteridae													
<i>Auchenipterichthys longimanus</i> (Günther 1864)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Centromochlus altae</i> Fowler 1945	*	*	*	*	*	*	*	*	*	*	*		X
<i>Tatia brunnea</i> Mees, 1974	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Tatia gyrina</i> (Eigenmann and Allen, 1942)	*	*	*	*	*	*	*	*	*	*	*	X	X
<i>Tetranematichthys quadrifilis</i> (Kner 1858)	*	*	*	*	*	*	*	*	*	*	*		X
Cetopsidae													
<i>Denticetopsis seducta</i> Vari, Ferraris & de Pinna 2005	*	*	*	*	*	*	*	*	*	*	*		X
<i>Helogenes marmoratus</i> Günther, 1893			7	5	4				5		21	X	
Doradidae													
<i>Physopyxis ananas</i> Sousa & Rapp Py-	*	*	*	*	*	*	*	*	*	*	*	X	

	Catchments										N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)	
	1	2	3	4	5	6	7	8	9	10				
Daniel, 2005														
<i>Physopyxis lyra</i> Cope, 1872	*	*	*	*	*	*	*	*	*	*	*	*		X
Trichomycteridae														
<i>Ituglanis amazonicus</i> (Steindachner, 1882)			2						1	1	4	X		
<i>Paracanthopoma</i> sp.	*	*	*	*	*	*	*	*	*	*	*			X
<i>Paravandellia</i> sp.	*	*	*	*	*	*	*	*	*	*	*			X
<i>Potamoglanis</i> cf. <i>hasemani</i> (Eigenmann, 1914)	*	*	*	*	*	*	*	*	*	*	*			X
<i>Tridens</i> sp.									2		2			X
<i>Tridentopsis</i> sp.	1										1			
Callichthyidae														
<i>Callichthys callichthys</i> (Linnaeus, 1758)	17	58	2	11				2	1		91			X
<i>Corydoras bilineatus</i> Knaack, 2002	327										327			
<i>Lepthoplosternum beni</i> Reis, 1997	67		1	16							84			X
<i>Megalechis picta</i> (Müller & Troschel, 1848)		4	3	9							16	X		X
Loricariidae														
<i>Acestridium discus</i> Haseman, 1911						9					9			
<i>Ancistrus</i> cf. <i>dubius</i> Eigenmann & Eigenmann, 1889	*	*	*	*	*	*	*	*	*	*	*			X
<i>Farlowella amazona</i> (Günther, 1864)	*	*	*	*	*	*	*	*	*	*	*			X
<i>Hemiodontichthys acipenserinus</i> (Kner, 1853)	*	*	*	*	*	*	*	*	*	*	*			X
<i>Otocinclus caxarari</i> Schaefer, 1997	*	*	*	*	*	*	*	*	*	*	*	X		
<i>Otocinclus mura</i> Schaefer 1997	*	*	*	*	*	*	*	*	*	*	*			X
<i>Parotocinclus amazonensis</i> Garavello, 1977	*	*	*	*	*	*	*	*	*	*	*			X
<i>Pterygoplichthys pardalis</i> (Castelnau, 1855)	4					1	2				7			
<i>Pterygoplichthys punctatus</i> (Kner, 1854)	1										1			
<i>Rineloricaria</i> cf. <i>formosa</i> Isbrücker & Nijssen, 1979			1								1			

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Rineloricaria cf. phoxocephala</i> (Eigenmann & Eigenmann 1889)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Rineloricaria lanceolata</i> (Günther 1868)	*	*	*	*	*	*	*	*	*	*	*		X
Heptapteridae													
<i>Gladioglanis conquistador</i> Lundberg, Bornbusch & Mago-Leccia, 1991		15	12					1	34	1	63	X	X
<i>Mastiglanis asopos</i> Bockmann, 1994	*	*	*	*	*	*	*	*	*	*	*		X
<i>Myoglanis koepcke</i> Chang, 1999	*	*	*	*	*	*	*	*	*	*	*		X
<i>Nemuroglanis cf. furcatus</i> Ribeiro, Pedroza & Rapp Py-Daniel, 2011						2					2		
<i>Rhamdella</i> sp.									1		1		
<i>Rhamdia cf. quelen</i> (Quoy & Gaimard, 1824)		17	5	83	2				1		108	X	
<i>Rhamdia muelleri</i> (Günther, 1864)	44										44		
Pseudopimelodidae													
<i>Batrochoglanis raninus</i> (Valenciennes, 1840)	*	*	*	*	*	*	*	*	*	*	*	X	X
Gymnotiformes													
Gymnotidae													
<i>Electrophorus electricus</i> (Linnaeus, 1766)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Gymnotus carapo</i> Linnaeus, 1758	1	3	12	19							35	X	X
<i>Gymnotus coatesi</i> La Monte, 1935	*	*	*	*	*	*	*	*	*	*	*	X	X
<i>Gymnotus coropinae</i> Hoedeman, 1962		44	2	23	10	3	1				83	X	X
<i>Gymnotus curupira</i> Crampton, Thorsen & Albert, 2005	2	1	13	10					1		27		
Rhamphichthyidae													
<i>Gymnorhamphichthys rondoni</i> (Miranda Ribeiro, 1920)						2					2	X	X
Hypopomidae													

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Brachyhypopomus batesi</i> Crampton, de Santana, Waddell & Lovejoy, 2017			11	3					2		16		
<i>Brachyhypopomus beebei</i> (Schultz, 1944)	4		6	6					5		21		
<i>Brachyhypopomus brevirostris</i> (Steindachner, 1868)		7									7	X	
<i>Brachyhypopomus hamiltoni</i> Crampton, de Santana, Waddell & Lovejoy, 2017	1	48	13	6					1		69		
<i>Brachyhypopomus sullivanii</i> Crampton, de Santana, Waddell & Lovejoy, 2017					3			1			4		
<i>Brachyhypopomus walteri</i> Sullivan, Zuanon & Cox Fernandes 2013	*	*	*	*	*	*	*	*	*	*	*		X
<i>Hypopygus lepturus</i> Hoedeman, 1962		5	69	18	4			3	16		115	X	X
<i>Microsternarchus bilineatus</i> Fernández-Yépez, 1968		11	19	26							56	X	X
<i>Steatogenys duidae</i> (La Monte, 1929)	*	*	*	*	*	*	*	*	*	*	*	X	X
Sternopygidae													
<i>Sternopygus macrurus</i> (Bloch & Schneider 1801)	*	*	*	*	*	*	*	*	*	*	*	X	X
Cyprinodontiformes													
Rivulidae													
<i>Moema cf. staECKi</i> (Seegers, 1987)	1								22	1	24		
<i>Pterolebias longipinnis</i> Garman, 1895	3								8		11		
<i>Anablepsoides atratus</i> (Garman, 1895)	55										55		
<i>Anablepsoides micropus</i> (Steindachner, 1863)	37	7	8	10	3						65	X	
<i>Anablepsoides ornatus</i> (Garman, 1895)	5										5	X	
<i>Anablepsoides taeniatus</i> (Fowler, 1945)	1										1		
<i>Laimosemion ubim</i> Costa & Lazzarotto, 2014	4			1							5		

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Laimosemion kirovskyi</i> Costa, 2004	24			19	12			1			56	X	
Beloniformes													
Belonidae													
<i>Belonion apodion</i> Collette, 1966			1					1			2		
<i>Potamorrhaphis eigenmanni</i> Miranda Ribeiro, 1915			1								1		
<i>Potamorrhaphis guianensis</i> (Jardine, 1843)	*	*	*	*	*	*	*	*	*	*	*		X
Synbranchiformes													
Synbranchidae													
<i>Synbranchus madeirae</i> Rosen & Rumney, 1972	3	11	1	2					1		18	X	X
<i>Synbranchus</i> sp.	20	2	12	3							37		X
Cichliformes													
Cichlidae													
<i>Acaronia nassa</i> (Heckel, 1840)	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Aequidens pallidus</i> (Heckel, 1840)	1			56							57		
<i>Aequidens plagiozonatus</i> Kullander, 1984	*	*	*	*	*	*	*	*	*	*	*		X
<i>Aequidens tetramerus</i> (Heckel, 1840)	134	13	19	26	2			1			195		X
<i>Apistogramma agassizii</i> (Steindachner, 1875)	149	45	438	42	19	10	13	7	6	13	742	X	X
<i>Apistogramma gephyra</i> Kullander, 1980	77		1			2	1				81		X
<i>Apistogramma pulchra</i> Kullander, 1980		37	11								48		
<i>Apistogramma regani</i> Kullander, 1980	*	*	*	*	*	*	*	*	*	*	*	X	
<i>Apistogramma resticulosa</i> Kullander, 1980	*	*	*	*	*	*	*	*	*	*	*		X
<i>Biotodoma cupido</i> (Heckel 1840)	*	*	*	*	*	*	*	*	*	*	*		X
<i>Crenicara punctulatum</i> (Günther, 1863)	*	*	*	*	*	*	*	*	*	*	*	X	X
<i>Crenicichla inpa</i> Ploeg, 1991		2	3	1				1			7	X	X
<i>Crenicichla johanna</i> Heckel, 1840	*	*	*	*	*	*	*	*	*	*	*		X
<i>Crenicichla regani</i> Ploeg, 1989	*	*	*	*	*	*	*	*	*	*	*		X
<i>Crenicichla semicincta</i> Steindachner, 1892	*	*	*	*	*	*	*	*	*	*	*		X

Catchments													
	1	2	3	4	5	6	7	8	9	10	N total	Barros <i>et al.</i> (2011)	Vieira <i>et al.</i> (2016)
<i>Laetacara thayeri</i> (Steindachner, 1875)	7						1		1	9	18		
<i>Laetacara cf. dorsigera</i> (Heckel, 1840)	2		1								3		X
<i>Satanoperca jurupari</i> (Heckel, 1840)	*	*	*	*	*	*	*	*	*	*	*		X
Eleotridae													
<i>Microphilypnus ternetzi</i> Myers, 1927			98								98	X	X
Polycentridae													
<i>Monocirrhus polyacanthus</i> Heckel, 1840	*	*	*	*	*	*	*	*	*	*	*		X
Number of specie by catchment	49	31	53	34	19	18	13	18	32	19			
Mean number of species by stream reach	17	17	12.2	6.75	9.2	9.5	6.75	7.5	19	13.5			
Number of specimens by catchment	2699	1368	4833	1184	477	251	185	188	872	509			

FIGURES

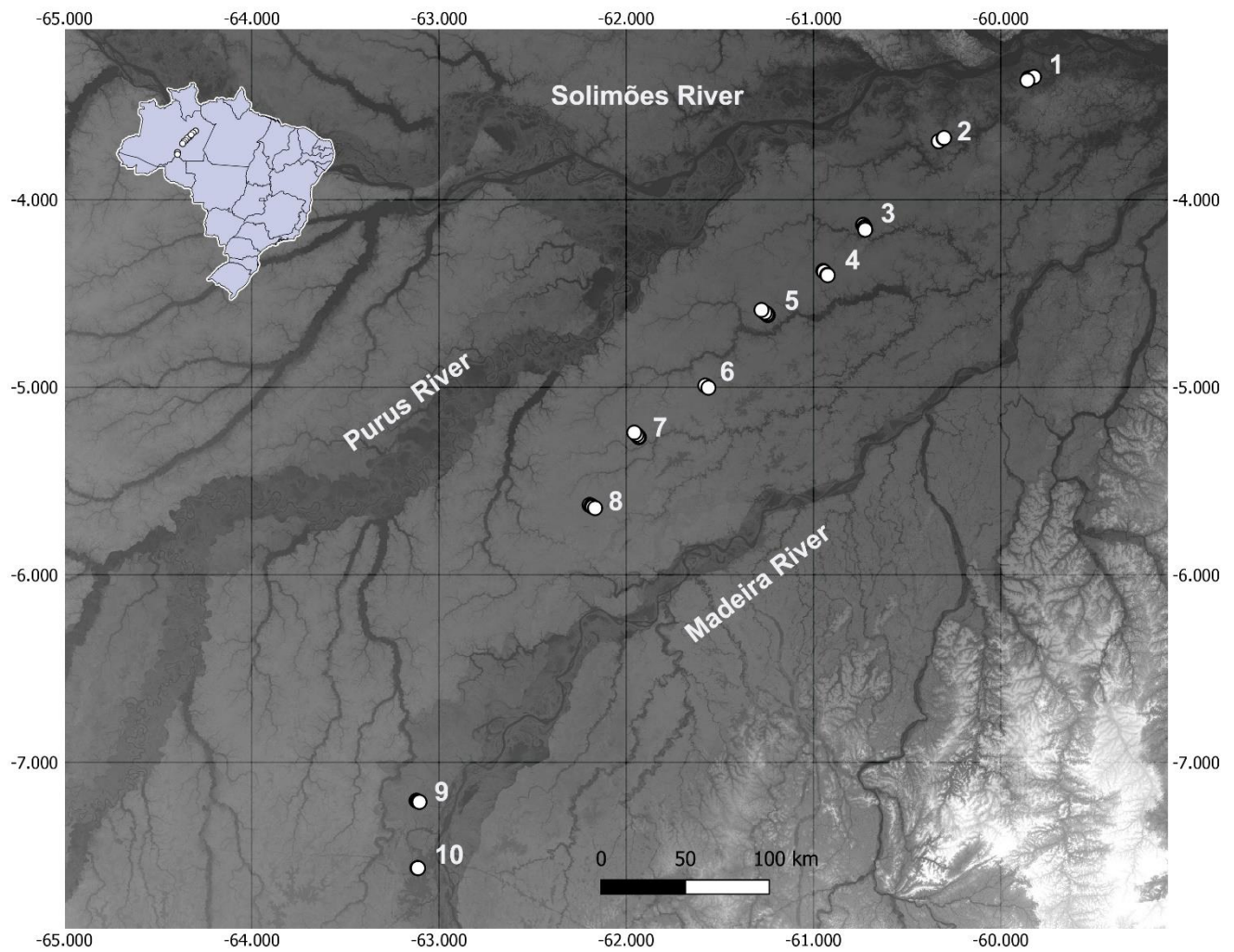


Figure 1. Elevation model of the study area showing the Purus-Madeira interfluvium in Central Amazonia, Brazil. White dots correspond to the 39 sampled streams, which are distributed in 10 catchments (numbers). Darker shades indicate lower altitudes (12 to 371 meters above sea level).

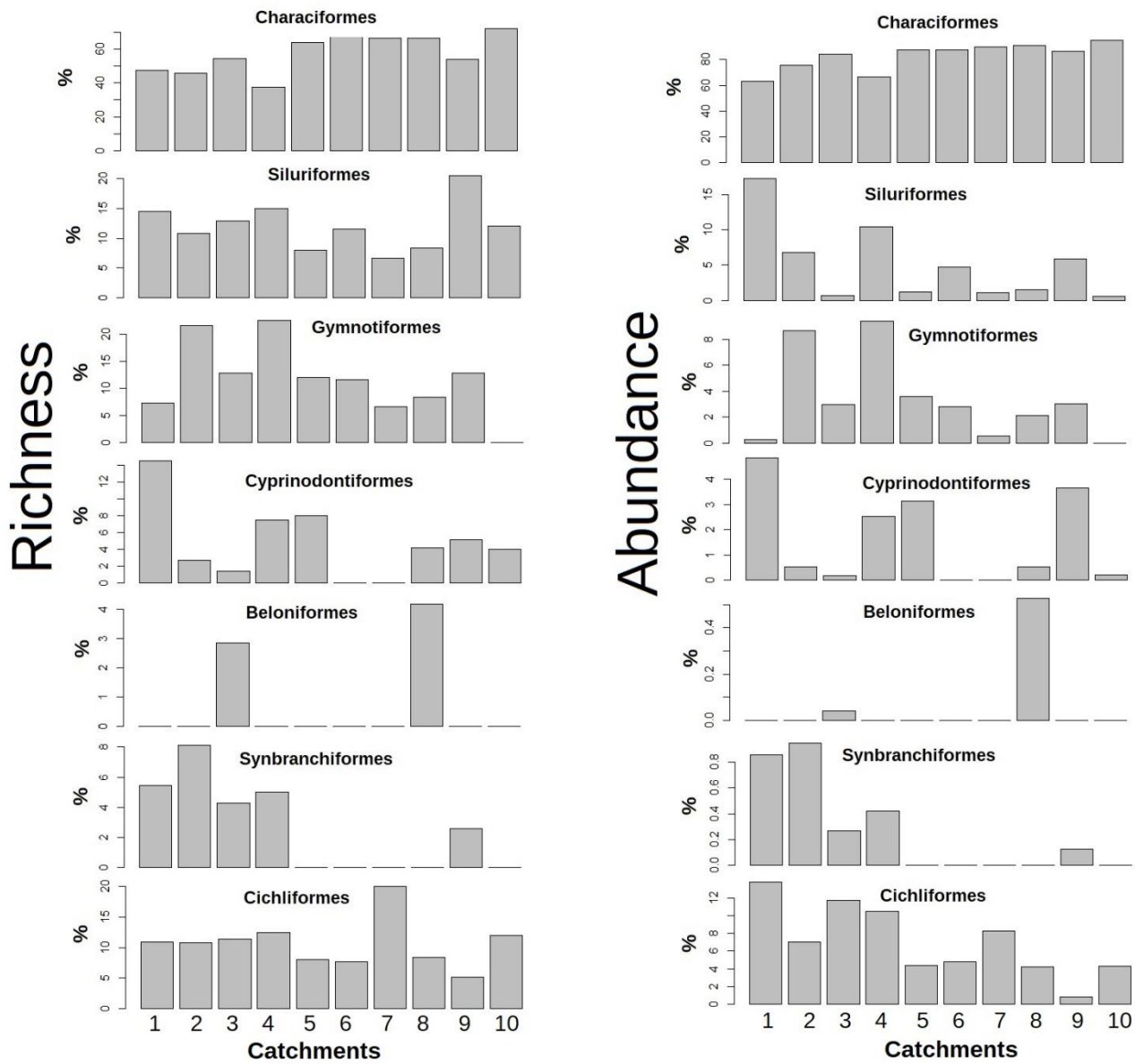


Figure 2. Proportion of fish species (left) and individuals (right) captured from each order in catchments studied in the Purus-Madeira interfluve.

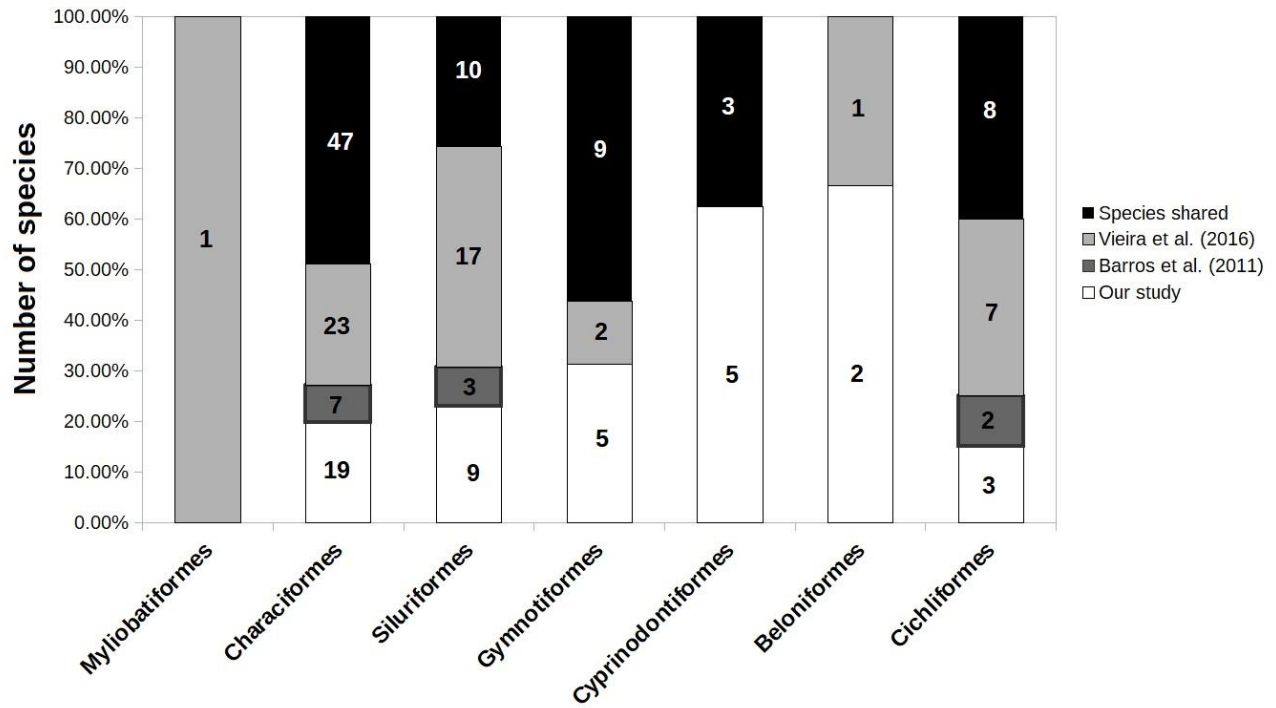


Figure 3. Proportion of species in each order found by each of the three major studies of small streams in the Purus-Madeira interfluvium. Numbers represent the number of species.



Figure 4. Representative species of fish recorded in Purus-Madeira interfluve. A. *Apistogramma agassizii*; B. *Bryconella pallidifrons*; C. *Laimosemion kirovskyi*; D. *Odonthocharacidum aphanes*; E. *Hemigrammus pretoensis*; F. *Copela callolepis*; G. *Nannostomus eques*; H. *Gladioglanis conquistador*; I. *Priocharax ariel*; J. *Dekeyseria scaphyhrinca*; K. *Laetacara thayeri*; L. *Moema cf. staecki*; M. *Callichthys callichthys*; N. *Hemigrammus melanochrous*; O. *Ituglanis amazonicus*; P. *Nannostomus marginatus*; Q. *Brachyhypopomus batesi*.



Figure 5. Representative species of fish recorded in Purus-Madeira interfluvium. A. *Brachyhypopomus beebei*; B. *Gymnotus curupira*; C. *Anablepsoides ornatus*; D. *Corydoras bilineatus*; E. *Crenuchus spilurus*; F. *Hypessobrycon* cf. *wosiackii*; G. *Copeina guttata*; H. *Apistogramma gephyra*; I. *Pyrrhulina laeta*; J. *Rineloricaria* cf. *formosa*; K. *Gasteropelecus sternicla*.

ARTIGO 2

The distance to large rivers affects fish diversity patterns in highly dynamic streams of Central Amazonia

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Abstract

Longitudinal-zonation hypotheses generally predict gradual changes in fish composition from upstream to downstream due to changes in habitat conditions, but largely disregard downstream effects on upstream segments. Floodplains of large rivers represent areas of high connectivity during flood periods and can act as stable refuges in dry seasons, which may attenuate deterministic constraints imposed by local conditions on fish assemblages in surrounding habitats. In this study, we investigated the effects of proximity to large rivers on taxonomic- and functional-diversity patterns of stream-fish assemblages in an extensive region of Central Amazonia. We sampled 31 headwater-stream reaches in nine catchments in the Purus and Madeira Rivers interfluvium between December 2014 and March 2015. Ninety seven fish species from seven orders and 19 families were captured. The results indicate that distance to large rivers is more important than distance among sites and local conditions in explaining functional and taxonomic diversity of stream-fish assemblages at large spatial scales. We also found a decrease in taxonomic and functional richness towards headwaters, mainly related to the loss of benthic and sedentary species along the distance gradient. These species may be favored by the proximity to refuge areas and high resource availability near the floodplain. In contrast, upstream assemblages were mainly occupied by small-sized, nektonic species with higher dispersal capacity, highly dependent of allochthonous resources. Downstream effects could be detected for many kilometers upstream in hydrographic catchments and this reinforces the crucial role of connectivity between fluvial habitats in maintenance of stream-fish diversity patterns in the region.

Introduction

Longitudinal fish zonation occurs when assemblages undergo changes along the linear gradient that connects upstream and downstream portions of a river network [1]. In general, increased availability and heterogeneity of habitats that occur along the longitudinal axis facilitate coexistence of species and the gradual accumulation of species in the downstream direction [1–5]. However, this

perspective disregards the effects of downstream habitats on upstream segments, which may limit deterministic constraints imposed by local conditions [6–9], especially for organisms with high dispersal abilities, such as fish that can transit between habitat patches. Therefore, freshwater assemblages are not determined solely by unidirectional effects [6,10–14] and physical disturbances and spatial arrangement are important elements maintaining some attributes of habitats and ecosystem functions [8,15].

Proximity to large rivers increases dispersal opportunities between habitats and availability of allochthonous resources, amplifying the role of mass-effects and source-sink dynamics in local and regional fish assembly [6,7,13,16]. Large-river floodplains provide greater environmental heterogeneity during high-water seasons, favoring lateral migrations and reducing competitive pressures [17]. The severity of hydrological disturbances in the dry season may depend on the spatial position of a stream within the drainage network and assemblages well connected to the floodplain should receive more migrants that buffer against demographic stochasticity and allow fast recovery from disturbance events [8,18]. Several studies have shown that low-order streams flowing directly into large rivers (i.e. adventitious streams) may have higher numbers of species than similar-sized streams located further up the network due to migration from the larger rivers [6,7,19,20]. Less well known are the effects of this connectivity on fish species that do not undertake large migrations, but are favored by lateral connectivity with marginal environments that allows them to avoid competitive pressures from species in the stream channel [21,22].

In a functional perspective, the river-continuum hypothesis predicts that headwater systems should be primarily occupied by small-sized and nektonic fish species mainly dependent on allochthonous resources, while downstream systems should harbor larger species predominantly supported by autochthonous production, especially for benthic fish guilds [5,12,23]. However, increased connectivity with large rivers can reduce effects of local filters on assemblages and increase opportunities for opportunistic migration of species that typically do not reside in low-order stream,

thereby increasing local functional richness [10,20]. Fish species also differ in their abilities to move through connecting waterways [24], and in strongly dynamic systems, where fish need to migrate following the water level, dispersal capacity can be a determining factor both to reach the refuges in the dry season and to recolonize new environments when the flow is reestablished [25]. Changes in functional structure of fish assemblages may facilitate the disentangling of effects of disturbances and habitat isolation as well as predicting potential changes in key ecological processes across the landscape [26,27].

Beta-diversity indices are useful tools to infer changes in species composition between sites and to identify the ecological gradients that structure these changes. Several methods have been proposed to partition the two main components of dissimilarity between habitats: species turnover and richness differences/nestedness [28,29]. Species turnover, or replacement, refers to simultaneous gains and losses of species in the landscape and can be linked to local conditions when species can move to favorable environments [30], or to stochasticity and drift when habitats are isolated and differences are accumulated across the landscape [31–33]. Richness differences or nestedness can reflect changes in resource availability or the effects of spatial filters [16,34]. Identifying the contribution of each dissimilarity component in different portions of a landscape allows better predictions about the ecological process acting on biological assemblages.

In this study, we investigate how proximity to large rivers determines the taxonomic and functional composition of fish assemblages in headwater systems in an extensive region of Central Amazonia. The region is characterized by a highly dynamic landscape where headwater streams can dry completely during drought months, and/or receive inputs from floodplains in the high-water season, depending on their distance to large rivers. We hypothesized that fish assemblages in similar-sized streams would differ in taxonomic and functional richness as a function of distance to large-river floodplain systems. This pattern should be determined mainly by the greater occurrence of species that benefit from the proximity to refuge areas and from the higher productivity of the floodplain, such as

detritivorous benthic and less dispersive species. In contrast, fish assemblages in streams further from large rivers should be dominated by species with better dispersal abilities and sustained by allochthonous food sources. We expected distance to the large rivers to be an important factor structuring stream-fish assemblages, and that streams similarly positioned in the drainage network would share a greater number of species and functional traits, regardless of local conditions and watercourse-distances among streams.

Methods

Study Area

Sampling was undertaken along 700 km of the Madeira-Purus interfluve, in southwestern Amazonas State, Brazil. The region is covered by dense rainforest with mean annual precipitation varying from 2000 to 2400 mm [35] (Fig 1). Predominant soil texture in the region is silt to fine sand and relief varies from flat to gently undulating, which results in poorly drained soils [35]. The combination of flat relief and high annual flood pulses of the Purus, Madeira and Amazon Rivers, which usually exceed 10 m [36], creates marginal lakes and temporally inundated systems during the wet season. However, the shallow water-table does not sustain surface flow in headwaters through consecutive drought months when the rain stops, causing smaller streams to dry completely for several weeks, or for free water to persist only in isolated pools along the stream bed. This hydrologic fluctuation determines a highly dynamic landscape, especially in headwater systems, which experience drought and flood conditions within short periods of time. We sampled 31 headwater-stream reaches (50-m long reaches in 1st to 3rd order streams) in nine catchments along the Madeira-Purus interfluve that drain to the Madeira or Amazon Rivers. The dense network is mainly non-hierarchical and the sub-basins can be short and flow directly to large rivers or be extensive and receive little influence from the floodplain of large rivers. Sampling was carried out in the first months of the rainy season, between

December 2014 and March 2015, when the streams returned to normal flow and the water level remained stable for months, allowing rapid recolonization of formerly dry stream channels. During the inundation phase, small streams overflow and vast areas are flooded, including parts of the road, making access difficult. These limitations make it hard to obtain more accurate information about the extent of flooding in terrestrial habitats. All stream segments sampled are permanent sampling plots of the Research Program in Biodiversity (PPBio) field-site network (<http://ppbio.inpa.gov.br/sitios/br319>).

Sampling

Stream-habitat variables

In each stream reach, we measured water temperature, electrical conductivity, dissolved oxygen and pH with a YSI Pro 10301 multiparameter probe. We also measured channel width, depth, substrate type and flow velocity in four transects perpendicular to the stream channel, separated from each other by 12.5m. Depth and substrate type were measured in nine equidistant points along each transect across the stream channel. Substrate was classified in one of six categories: sand, clay, trunk (wood with diameter >10 cm), coarse litter (leaves and small branches), fine litter (organic silt) or roots (fine roots from riparian vegetation). Flow velocity was estimated as the average time that a floating object took to travel 1 m, replicated three times. For statistical analyses, we use the average values of channel width, depth, flow velocity and the percentage of each substrate type of each stream reach. For details regarding the environmental-sampling protocol see [37].

Fish sampling

In each stream, the 50-m long reach was isolated with block nets (5mm mesh) and fish were caught using seines and hand nets. Although 100 to 150-m stream sections have been used for stream-fish studies, the use of 50-m long stream reaches allows robust inferences regarding both taxonomic and functional fish diversity in such water bodies (see the sensitivity analyses provided by the

electronic supplementary material S5 in [26]). Sampling larger segments of first-order streams reduces the precision of predictor variables, such as stream depth, because streams may become very small or disappear over distances of 100m [38], and the extra precision in description of fish assemblages does not compensate for the reduction in replication due to time constraints for sampling in this area of difficult access. Furthermore, repeated sampling over nearly 20 years in 50-m reaches of upland forest streams have revealed a high stability and predictability of local fish assemblages, that support the use of such stream-reach size for ecological analyses (JZ pers. observations in Reserva Ducke near Manaus, Amazonas state, Brazil, between 2001 and 2019).

Fish were collected only during the day and collection effort in each section was standardized by using two collectors over two hours. The specimens were euthanized in clove-oil solution, which decreases fish neurosensory functions by acting upon the nervous systems. The specimens were fixed in 10% formalin and preserved in 70% ethanol. Fishes were sorted, counted and identified to species level in the laboratory using dichotomous keys and specialized literature, such as [39], [40], [41] and [42]. All collected specimens were deposited in the fish collection of the Instituto Nacional de Pesquisas da Amazônia (INPA). The sampling procedures were approved by INPA's Institutional Committee for Ethics in the Study of Animal (Comissão de Ética no Uso de Animais #052/2012) and a research license was provided by the Brazilian Institute of the Environment and Renewable Natural Resources (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, SISBIO#10.199-1).

Functional traits

Each fish species was functionally characterized with respect to locomotor ability, habitat use and food intake. Body mass and morphometric measurements were taken from 3–10 adult individuals per species and then combined in 13 ecomorphological traits (see S1 Text and S2 Table for details). The functional traits were used to calculate a pairwise functional distance between species using Euclidian

distance. We then ran a principal components analysis (PCA) on the functional-distance matrix to obtain the coordinates of the species in multidimensional space. To define the number of dimensions that best describes the functional space, we used the framework developed by [43], which analyzes the congruence between the initial functional distance (Euclidian distance matrix) and the distance between each pair of species in the functional space. This indicated that the first four PCA axes used to build the functional space closely reflected the initial functional dissimilarity between species (mean squared deviation between functional standardized distance and initial distance <0.001). Therefore, we kept the first four axes to describe the functional space, representing 76.1% of the inertia. We had to exclude two assemblages with less than four species due to computational requirements (i.e. higher number of species than PCA axes), as proposed by [44].

To evaluate how functional space varies between fish-assemblages, we computed the functional-richness index (FRic), which represents the amount of functional space filled by all species within the assemblage, indicating the range of trait combinations or niche occupation [41]. To investigate how functional-trait values vary in each assemblage, we calculated the community-weighted mean (CWM hereafter) of each trait, which represents the average value of each functional trait in the assemblage based on the occurrence of the species and their relative abundances. The indices were calculated using the script “FD” developed by [45] using R software [46].

Beta-diversity indices

We calculated the variation in taxonomic species composition (Taxonomic Beta Diversity, hereafter $T\beta_{s\text{or}}$) among the 31 stream reaches by means of pairwise comparisons using Sørensen-based index developed by [47] for use with presence/absence data. To evaluate the role of the different ecological processes on spatial variation among fish assemblages, we decomposed the Sørensen-based index in relativized richness difference (species gains and losses, $T\beta_{\text{rich}}$) and relativized species replacement ($T\beta_{\text{repl}}$). We chose the $T\beta_{\text{rich}}$ instead of the nestedness component [48] because the first

incorporates several compositional differences attributable to richness and not only those due to nestedness [29]. The beta-diversity indices were computed using the script proposed by [29] using R software.

Variation in functional diversity between stream reaches (hereafter $F\beta_{s\sigma r}$) was calculated from pair-wise intersections between convex hulls in a multidimensional functional space created with the first four PCA axes using the Sørensen dissimilarity index. $F\beta_{s\sigma r}$ was decomposed into functional turnover ($F\beta_{sim}$) and functional nestedness ($F\beta_{nes}$), following the framework proposed by [44]. Functional turnover is measured as the amount of overlap in functional space between two assemblages, and the functional nestedness represents the amount of functional space of one assemblage that is filled by another [44]. The indices were calculated from the “betapart” package developed by [49] using R software.

Geographical and abiotic predictors

To test the effect of distance to large rivers on diversity patterns, we measured the distance between each stream reach and the nearest large river (Madeira or Amazon Rivers) following the watercourse. The distances were calculated by summing the lengths of segments between each stream reach and the nearest large river in a GIS hydrological framework developed by [50] using QGIS 2.6 software. The distance measurements for each stream reach are given in S1 Table. We used these data to create a dissimilarity matrix using Euclidian distances (differences in distance to large rivers).

To evaluate the effect of watercourse distance on taxonomic and functional patterns, we calculated the network distance between each pair of stream reaches using the QNEAT3 extension for QGIS Network Analysis in the GIS hydrological framework developed by [50]. We also calculated the linear distance between sites since the flat relief of the study area permits the overflow of small streams during flood seasons, possibly connecting them through the floodplain environment and allowing dispersal outside the main stream courses. The two distance matrices were highly correlated (Mantel

statistic $r = 0.89$) so we used only watercourse distance as it represents a more usual measure in riverine landscape studies. To describe the differences in the local conditions of the streams, we calculated a dissimilarity matrix with Euclidean distances on standardized abiotic variables.

Statistical analyses

All statistical analyses were carried out using R software [46]. The relationships between the components of $T\beta s\sigma r$ and $F\beta s\sigma r$ and the predictor variables (difference in distance to larger rivers, watercourse distance and dissimilarity in local conditions) were assessed by matrix correlation using Mantel tests. Since the matrices of difference in distance to large rivers and watercourse distance are correlated (Mantel $R = 0.59$; $P = 0.001$), we used a partial Mantel correlation to control possible confounding effects and to assess the individual contribution of each matrix. This statistic computes the degree of relationship between assemblage dissimilarities and each predictor matrix while controlling for the effect a third potentially confounding variable. This is achieved by regressing each matrix on the third one and then computing a Mantel test with the residuals of the regressions [51]. This does not fully control the possible effects of spatial autocorrelation, but rather dissociates the effects of watercourse distance from the effects of differences in distance to large rivers on assemblage dissimilarities. We also used a partial mantel test to control the effects of local conditions on beta diversity indices. Mantel and partial Mantel tests were calculated using the “vegan” package [46].

Similarities within catchments could cause autocorrelation, so we also provide a partial Mantel test to examine the relationships between the beta diversity components and the predictor variables, including a catchment identity matrix as confounding factor to ensure that significant correlations are not determined by autocorrelation effects due to greater similarities within catchments. The catchment identity matrix consists of a dissimilarity matrix where pairwise comparison of stream reaches from the same catchment had value equal to zero and comparisons between streams of different catchment have had a value equal to one. The analysis results are given in S2 Text.

To evaluate how local conditions interact with distance to large rivers to determine functional characteristics of stream-fish assemblages, we summarized the effects of local conditions with a Principal Component Analyses (PCA) for the standardized abiotic variables and retained the first axis as a descriptive variable, which represented 52% of variation in local conditions. The loading values for each variable are given in S1 Table. Then we used the first PCA axis and the distance to large rivers as fixed effects in a linear mixed-effect model (LMM) for Functional Richness (Fric), taxonomic richness and all CWM values of each assemblage. Catchment was included in the model as a random variable to account for the nested design (stream within catchment). LMM analyses were conducted with the package “lme4” and the marginal and conditional R² were calculated using the package “MuMIn” [46]. We also calculated the Moran’s I values using the residuals of linear mixed-models to evaluate if the significance of the relationship that we found is affected by spatial autocorrelation and the results are given in S2 Text

Results

A total of 97 fish species from seven orders, 19 families and 57 genera were captured. Characiformes was the richest order with 52 species, followed by Siluriformes (14 species) and Gymnotiformes (12 species); the remaining 19 species were from four orders (Fig 2; S2 Table for details). Taxonomic richness ranged from 4 to 24 species per stream reach and 33 species were collected only once. Only four species were collected in more than 50% of streams (*Copella callolepis*, *Apistogramma agassizii*, *Crenuchus spilurus* and *Hemigrammus melanochromis*, in decreasing order of participation). Most species found in the streams were small-sized fishes typical of headwater systems and almost 75% of species had adult standard length less than 15 cm.

We found a significant positive correlation between taxonomic beta diversity ($T\beta_{sor}$) and distance to large river, mainly associated with the richness component ($T\beta_{rich}$) (Fig 3). The partial Mantel tests indicated that this association was maintained even after controlling for the effect of

watercourse distance and local abiotic effects (Table 1) and after controlling the effects of catchment identity (S2 Text). This indicates that streams similarly connected to floodplain systems are also similar in fish-assemblage composition, regardless of watercourse distance. There also appeared to be an effect of watercourse distance on richness differences ($T\beta_{rich}$), but this association was not statistically significant after controlling for the effects of distance to large rivers (Table 1).

Few species occurred continuously along the connection gradient to large rivers, indicating a strong pattern of substitution between catchments (Fig 2), and the beta-diversity analysis indicated that the variability in fish assemblages was more a result of species substitution ($T\beta_{repl} = 67\%$ of total beta diversity) than loss or gain of species ($T\beta_{rich} = 33\%$). However, we found no clear relationship between the turnover component ($T\beta_{repl}$) and any predictor variables (Table 1). We also found no significant correlation between the taxonomic beta-diversity index and differences in local conditions.

In accordance with the Mantel tests, the LMM results indicated that distance to large rivers had a negative effect on richness of stream-fish assemblages (Table 2; Fig 4). The histogram of species frequency (Fig 2) shows a clear decrease in the number of species along the connection gradient to large rivers and a near disappearance of species of Synbranchiformes and Cyprinodontiformes in the upstream reaches.

There was a significant correlation between the functional beta-diversity index ($F\beta_{sor}$) and difference in distance to large rivers (Table 1), indicating that stream position influences the functional similarity patterns of the local fish assemblages. However, the difference in functional composition was not significantly related to either nestedness ($F\beta_{nes}$) or turnover ($F\beta_{sim}$) components. Despite the lack of relationship between $F\beta_{nes}$ and distance to large rivers, we found a decrease in functional richness in the upstream direction, indicated by the LMM results (Table 2; Fig 4), and there was no statistically-significant spatial autocorrelation in the LMM residuals (S2 Text). This indicates that the functional space, besides decreasing in upstream direction, is also changing along the gradient, thus preventing assemblages with greater functional richness completely filling the functional space of others and

determining functional nested patterns. We found no relationship between local conditions and taxonomic or functional richness (Table 2).

The LMM results showed a significant relationship between the fish functional traits body mass (LogM), body transversal surface (Bsf) and aspect ratio of the pectoral fin (PFar), and distance to large rivers, indicating that assemblages from streams far from large rivers are mainly composed by smaller-sized species with greater swimming ability that inhabit the upper and middle layers of the water column (Fig 5). Furthermore, some traits linked to prey-detection ability (Eps, Edst) and feeding strategy (Osh) were significantly related to distance to large rivers. Stream assemblages closer to large rivers had a higher proportion of species with downturned mouths and low-positioned eyes, indicating an increase in importance of detritivorous habits. There was a higher proportion of species with terminal to superior mouth and laterally positioned eyes (mostly drift feeders on allochthonous food sources) in streams located towards headwaters and far from large rivers. Oral-gape position was the only functional trait significantly related to local abiotic conditions (1st PCA) (Table 2). That axis was mainly related to percentage of coarse litter, mean depth and mean width (more details in S1 Table).

Discussion

The results corroborated our hypothesis that, at large spatial scales, differences in connection to large rivers are more important than watercourse distance and local conditions in determining functional and taxonomic dissimilarity between stream-fish assemblages. The longitudinal fish zonation that we found is mainly determined by the increase in taxonomic and functional richness close to large rivers and cannot be attributed to an increase in local habitat availability, since all streams are positioned at the headwaters of their respective catchments and are of similar physical dimensions. Similarity within catchments could result in autocorrelation, but the fact that catchments similarly positioned in relation to large rivers, such as catchments 1 and 9, share species and richness patterns is strong evidence of structuring processes unrelated to geographical proximity and the significance

values of tests are not affected by autocorrelation, because there was no significant autocorrelation in the residuals of the linear mixed models (S2 Text). This reinforces the hypothesis that stream position in the hydrological network affects the degree of influence of downstream systems on upstream structural patterns through dispersal-mediated interchanges between habitats types, as has been demonstrated in other studies [6,7,10,15,20]. None of the analyzed streams flowed directly into a large river, but the pattern that we found shows that these effects can be detected for many kilometers upstream in the hydrographic catchments that compose a main river basin.

Proximity to floodplains seems to be one of the main factors favoring the constitution of assemblages with higher species richness close to large rivers, since flood pulses allow dispersal that increases the lateral connectivity and the heterogeneity of resources and habitats [20,22,52–54]. Furthermore, most species that inhabit the small streams may be forced to migrate following the retraction of the water level during the dry season, probably using the shallow banks of the larger water courses as refuge areas. These environments are likely to be more available and predictable close to the floodplains and can act as additional habitats for some species, expanding areas for foraging and shelter. These seasonally-available conditions may allow the maintenance of larger local populations and reduce rates of density-dependent mortality [13,54]. Long-term ecological studies in intermittent environments in Central Amazonia are fundamental to better understand the influence of seasonality on local assemblage structure.

Functional changes in fish assemblages along the longitudinal gradient have been frequently reported, mainly related to changes in local conditions [2,5,12,55]. Although largescale studies are more apt to detect regional than local effects [53], the lack of relationship between the functional patterns and the abiotic conditions in our study is an indication that fish-assemblage structure is not limited by local nutrient dynamics but is also influenced by the ecological processes that occur in surrounding environments [54]. An example is the high frequency of more sedentary and benthic species in stream reaches close to large rivers. These guilds feed on small aquatic invertebrates and/or

decomposing material in bottom deposits and are highly dependent on processing of the organic matter in upstream reaches [5,42]. These results indicate that floodplains can buffer the limitation imposed by local conditions and act as a core area for sedentary and benthic species and the accumulated effects of high recruitment of these guilds from the floodplain can be detected at large distances upstream.

Small-sized or miniature species, such as those of the genera *Microcharacium*, *Axelrodia*, *Tythocharax*, *Xenurobrycon*, *Nemuroglanis* and *Priocharax*, were predominant in the assemblages of the most isolated streams. Miniature species rarely live longer than one year in the wild and low nutrient levels in their natural habitats may limit body development of these lineages, which do not exceed 26 mm standard length as adults [56]. The lack of accurate information on the life history of these species makes it difficult to understand their distribution patterns, but it is possible that low dispersal capacity coupled with less nutritional requirements and weaker predation pressure are keeping these species confined to the more isolated headwater drainages [57]. Large-bodied sedentary species, such as members of the genera *Hoplerythrinus*, *Synbranchus*, *Pterygoplichthys*, *Leptoplosternum* and *Gymnotus*, did not occur in the stream reaches furthest from the large rivers. These species are occasionally caught in low-order streams [20, 42] but do not establish large populations there, only using small streams opportunistically as feeding and shelter areas. These species are likely to be heavily dependent on large water bodies for the maintenance of viable populations.

Our results highlight the importance of connectivity between small catchments and riverfloodplain systems for the maintenance of stream-fish assemblage composition, diversity and functional characteristics. The fact that the drainages studied are exposed to seasonal droughts may amplify the role of dispersal in structuring of local assemblages and select species capable of reaching favorable environments throughout the catchment [58–59]. The patterns found show that stream-fish assemblage structure varies according to the drainage position and that generalizations about the ecosystem services provided by fish assemblages in headwaters systems can be inaccurate if they do not incorporate the influence of downstream reaches on upstream assemblages. These findings

constitute the baseline to understand the mechanisms that regulate fish movements in the Purus-Madeira interfluve, a threatened region due to the repaving of the BR 319 highway [60]. Future studies of dispersal patterns throughout the catchment and the level of permeability of the landscape to the fish fauna are fundamental to improve our understanding of the probable environmental impacts of road construction on these aquatic ecosystems and to devise effective strategies for protection and monitoring.

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TABLES

Table 1. Summary of the Mantel correlations (r values) from Mantel tests and Partial-Mantel tests between functional and taxonomic beta-diversity of stream-fish assemblages and predictor variables. (A) and (E): Simple Mantel test. (B) and (F): Partial Mantel tests controlling the effects of differences in distance to large river. (C) and (G): Partial Mantel tests controlling the effects of watercourse distance. (D) and (H) Partial Mantel tests controlling the effects of dissimilarity in local conditions. Bold values correspond to statistically-significant correlations. * $p < 0.05$; ** $p < 0.005$.

			Distance to large rivers difference	Watercourse distance	Local conditions dissimilarity
Taxonomic diversity	Simple Mantel	T β sør (A)	0.293**	0.187*	0.005
		T β rich	0.335**	0.236*	0.029
		T β repl	-0.060	-0.06	-0.022
	Partial Mantel	T β sør (B)	-	0.016	-0.049
		T β rich	-	0.048	-0.030
		T β repl	-	-0.027	-0.012
		T β sør (C)	0.230**	-	-0.054
		T β rich	0.249*	-	-0.039
		T β repl	-0.034	-	-0.008
		T β sør (D)	0.297**	0.200*	-
T β rich	0.335**	0.242*	-		
T β repl	-0.060	-0.055	-		
Functional diversity	Simple Mantel	F β sør (E)	0.222*	0.057	0.207
		F β nes	0.044	0.027	-0.061
		F β sim	0.088	0.009	0.171
	Partial Mantel	F β sør (F)	-	-0.085	0.168
		F β nes	-	0.002	-0.072
		F β sim	-	-0.049	0.159
		F β sør (G)	0.230*	-	0.183
		F β nes	0.035	-	-0.078
		F β sim	0.101	-	0.201
		F β sør (H)	0.186*	-0.029	-
F β nes	0.059	0.057	-		
F β sim	0.053	-0.066	-		

Table 2. Probability associated with each predictor variable in the linear mixed-effects models (LMM) for CWM values and functional and taxonomic richness as functions of the distance to large rivers and local abiotic conditions (1st PCA axis). Catchment was considered a random effect in all models. Marginal R² (R² marg) values are for the models adjusted only considering fixed effects, and the conditional R² (R² cond) corresponds to the full model, including the random effects. Bold values correspond to p<0.05. LogM = log (body mass+1); Osh = Oral-gape shape; Ops = Oral-gape position; Edst = Eye size; Eps = Eye position; Bsh = Body transversal shape; Bsf = Body transversal surface; PFps = Pectoral-fin position; PFar = Aspect ratio of the pectoral fin; CPt = Caudal-peduncle throttling; Frt = Fin-surface ratio; Fsf = Fin-surface to body-size ratio; Cfar = Aspect ratio of the caudal fin.

Relative contribution of predictor variables					
		Distance to large rivers	Abiotic conditions (1 st PCA)	R ² marg	R ² cond
Depend variables	Taxonomic Richness	0.008	0.207	0.419	0.674
	Functional Richness	0.010	0.34	0.283	0.409
	LogM	0.048	0.42	0.229	0.61
	Osh	0.003	0.3	0.268	0.268
	Ops	0.295	0.001	0.308	0.574
	Edst	0.026	0.58	0.167	0.189
	Eps	0.024	0.27	0.223	0.384
	Bsh	0.880	0.35	0.036	0.157
	Bsf	0.021	0.32	0.305	0.684
	PFps	0.055	0.088	0.188	0.283
	PFar	0.010	0.79	0.226	0.304
	CPt	0.081	0.4	0.172	0.515
	CFar	0.170	0.76	0.1	0.281
	Frt	0.220	0.38	0.061	0.061
	Fsf	0.990	0.21	0.056	0.39

FIGURES

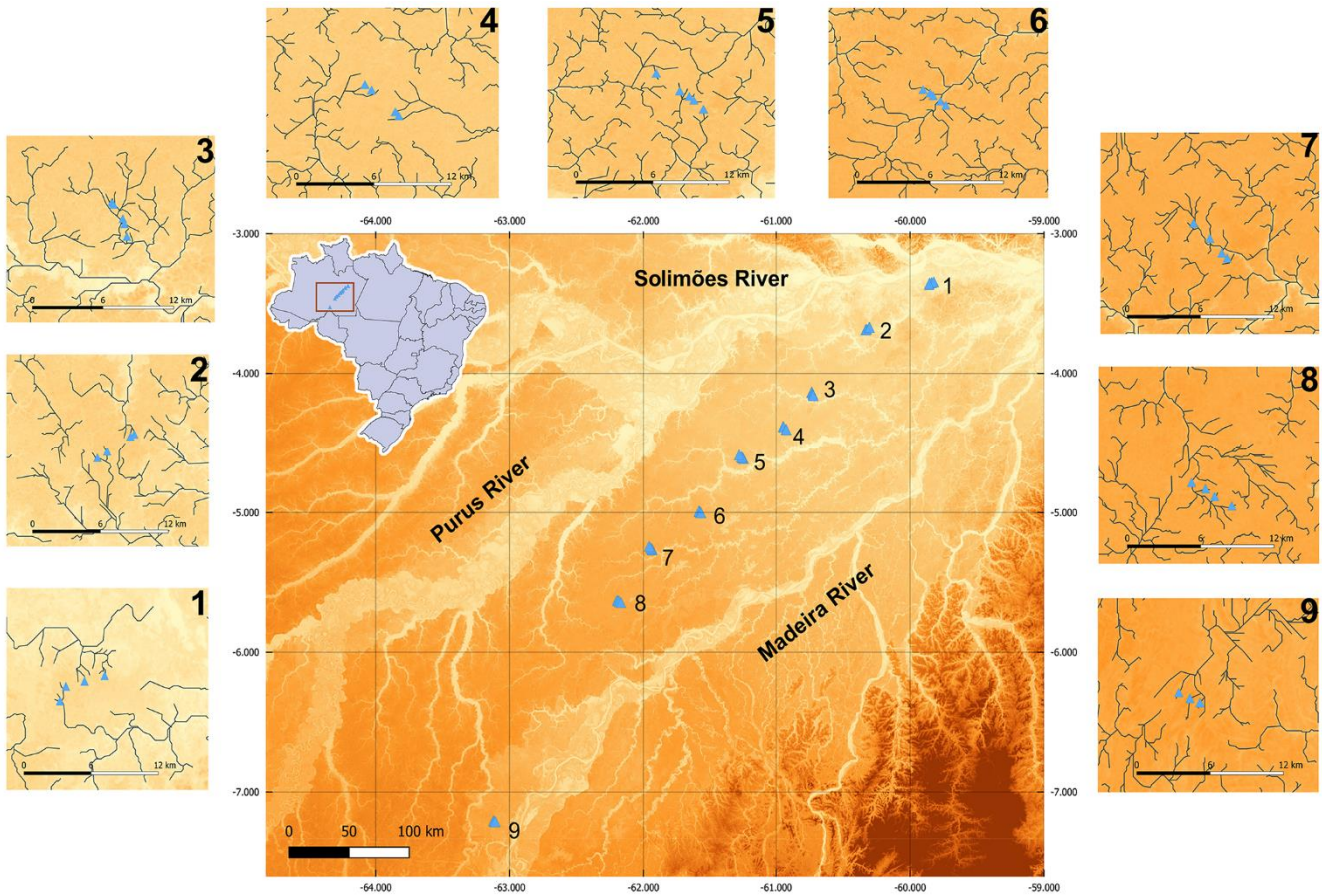


Figure 1. Elevation model of the study area showing the Purus-Madeira interfluvium in Central Amazonia, Brazil. Blue triangles correspond to the 31 sampled streams, which are distributed in nine catchments (numbers). Smaller figures show each sampled catchment in detail. Darker shades indicate higher altitudes (12 to 371 meters above sea level).

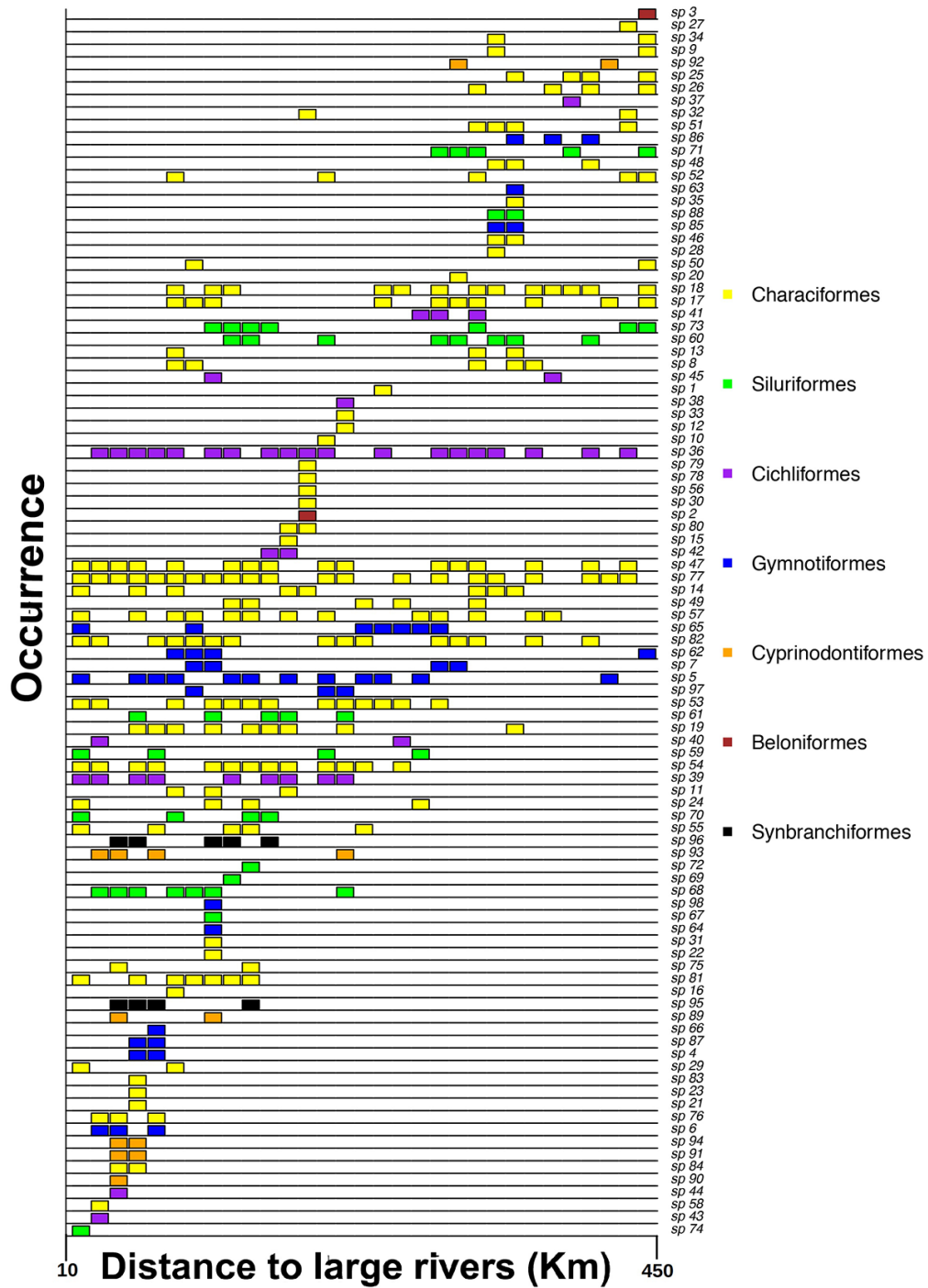


Figure 2. Fish species occurrence based in presence/absence data in 31 stream reaches ordered by the gradient of distance to large rivers. Different colors represents different fish orders. See supporting information Table S2 for full species names.

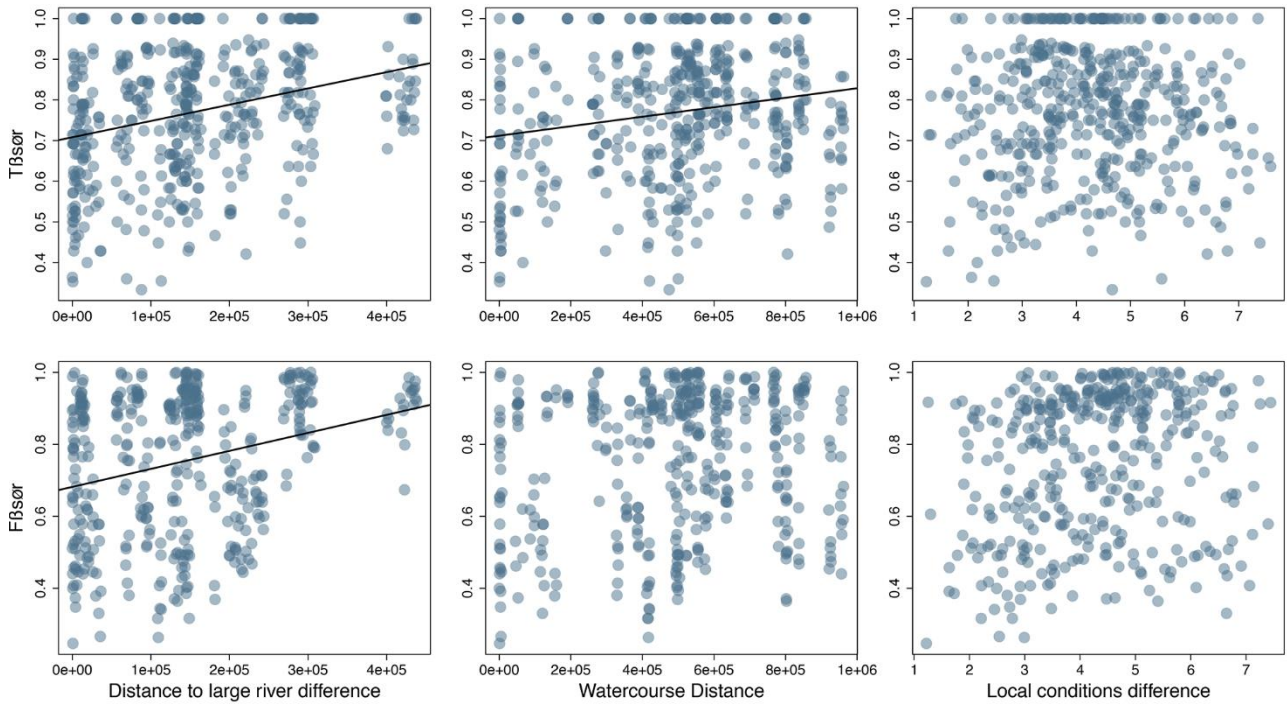


Figure 03. Relationships between taxonomic ($T\beta_{s\text{ør}}$) and functional ($F\beta_{s\text{ør}}$) beta diversity and distance to large rivers difference, watercourse distance and local-condition differences. Fitted lines indicate probabilities <0.05 .

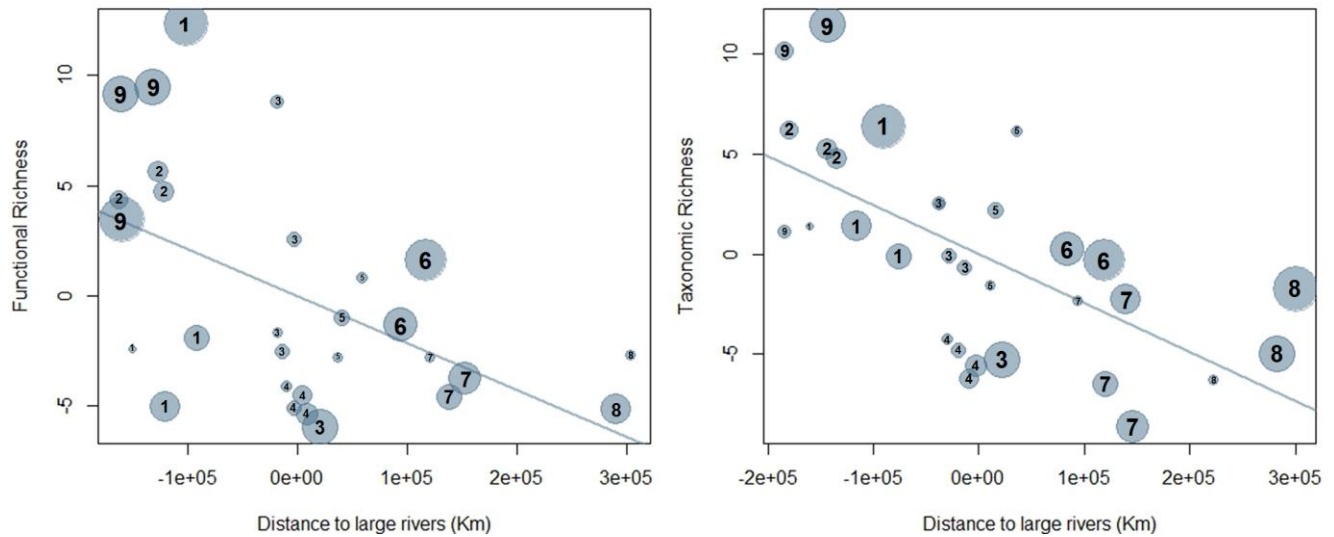


Figure 4. Partial regression derived from the linear mixed-effects models (LMM) investigating the effects of distance to large rivers on the functional and taxonomic richness of local stream-fish

assemblages. Distance to large rivers ranged from 10 to 449 km. Circle size indicates the mean width of each stream reach and numbers represents the catchments (S1 Table for details).

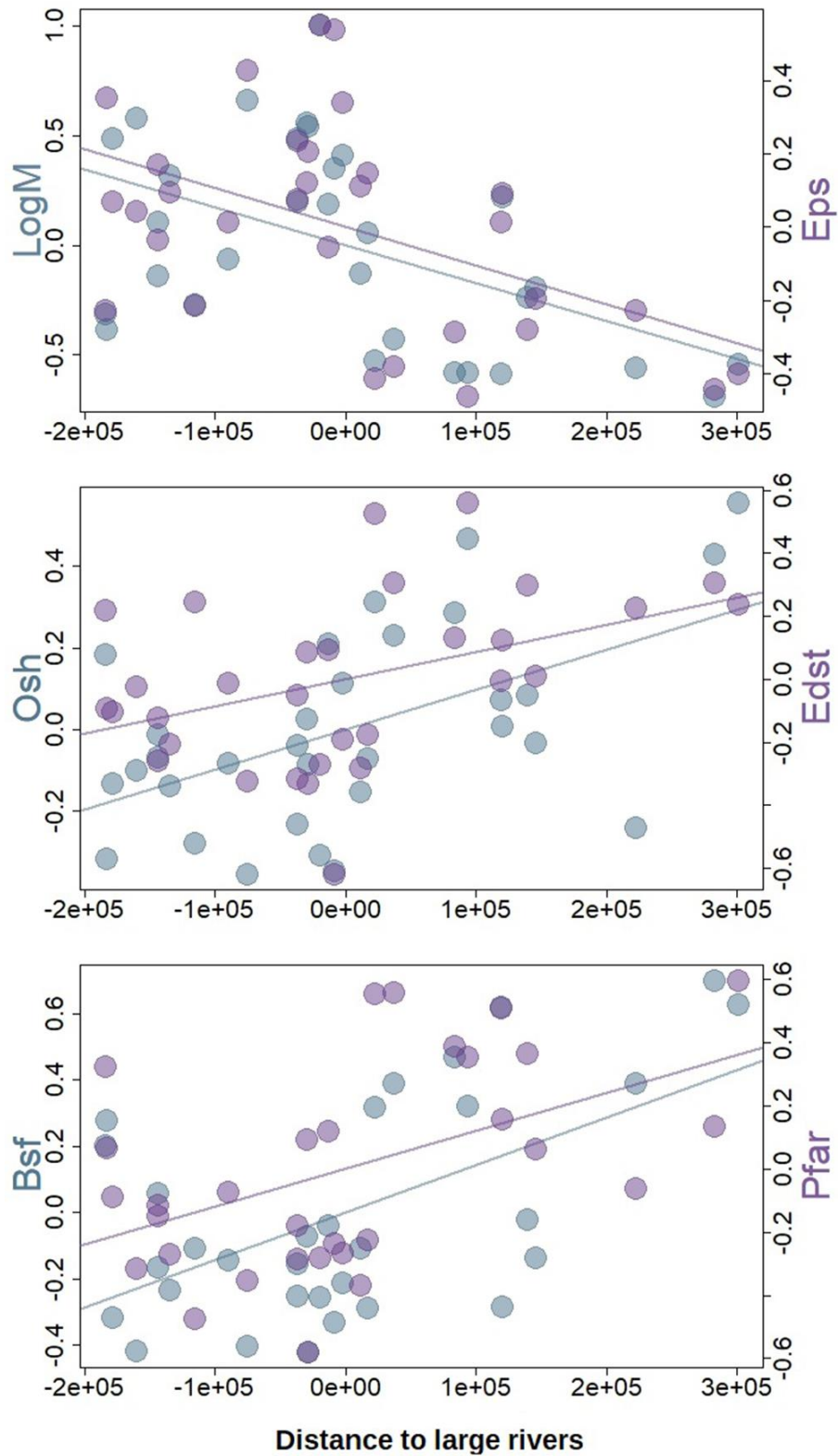


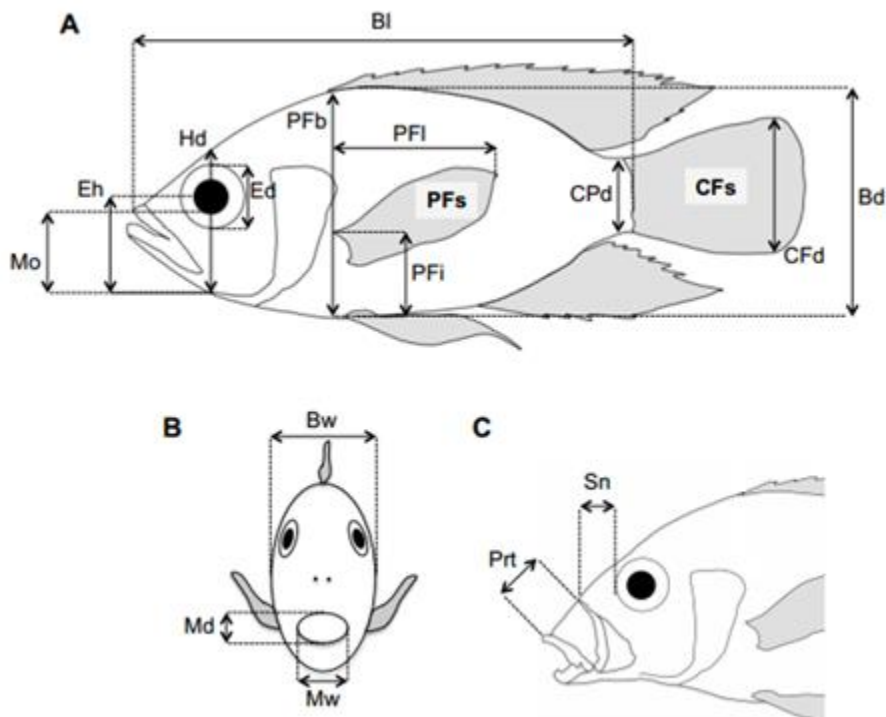
Figure 5. Partial regression derived from the linear mixed-effects models (LMM) investigating the effects of distance to large rivers on CWM with fixed-effect probabilities < 0.05 . More details about calculations of functional indices are given in S1 Text. LogM = $\log(\text{body mass}+1)$; Eps = Eye position; Edst = Eye size; Osh = Oral-gape shape; Bsf = Body transversal surface; PFar = Aspect ratio of the pectoral fin. Distance to the large rivers ranged from 10 to 449 km (See S1 Table for details).

ARTIGO 2 – MATERIAL SUPLEMENTAR

Appendix S1 text: Functional-trait measurements

The functional data used were extracted from an extensive morphometric functional database for Amazonian stream fishes developed by the Igarapés Project. Body mass and morphometric measures were taken on 5 to 12 individuals per species (figure 1) and then combined into ecomorphological traits (Table 1). These traits, except the log-transformed mass, are expressed as unit-less ratios to prevent trivial correlation with body-size. The specimens were weighed using an electronic balance (0.001 g). Body width, mouth width, mouth depth, snout length and protrusion length were measured with a digital caliper (limit of reading 0.1 mm). The other morphological measures were obtained through the use of digital pictures analyzed in Image J software (limit of reading 0.1 mm). We chose 13 functional traits that allowed us to evaluate the functional structure of fish assemblages by characterizing species for three key functions: food acquisition, locomotion, and habitat use.

Figure 1. Fish morphological traits measured from digital pictures



Bd - body depth, CPd - caudal-peduncle minimal depth, CFd - caudal-fin depth, CFs - caudal-fin surface, PFi - distance between the insertion of pectoral fin to the ventral profile, PFb - body depth at the level of the pectoral-fin insertion, PFI - pectoral-fin length, PFs - pectoral-fin surface, Hd - head depth along the vertical axis of the eye, Ed - eye diameter, Eh - vertical distance between the center of the eye and the ventral profile of the head, Mo - distance from the top of the mouth to the ventral profile of the head along the head depth axis; and with digital caliper (B, C): Bw - body width, Md - mouth depth, Mw - mouth width, Sn - snout length, Prt - protrusion length.

Table 1. List of 13 functional indices calculated from the species ecomorphological traits.

Functional trait	Calculation	Abbreviation	Ecological meaning	Reference
Oral-gape shape	$\frac{Md}{Mw}$	Osh	Way to capture food items	Karpouzi and Stergiou [1]
Oral-gape position	$\frac{Mo}{Hd}$	Ops	Feeding tactic in the water column	Adapted from Sibbing and Nagelkerke [2]
Eye size	$\frac{Ed}{Hd}$	Edst	Prey detection	Adapted from Boyle and Horn [3]
Eye position	$\frac{Eh}{Hd}$	Eps	Vertical position in water column	Gatz [4]
Body transversal shape	$\frac{Bd}{Bw}$	Bsh	Vertical position in water column and hydrodynamism	Sibbing and Nagelkerke [2]
Body transversal surface	$\frac{\ln\left[\left(\frac{\pi}{4} * Bw * Bd\right) + 1\right]}{\ln(Mass + 1)}$	Bsf	Mass distribution along the body for hydrodynamism	Villéger <i>et al.</i> , [5]

Pectoral-fin position	$\frac{PFi}{PFb}$	PFps	Pectoral-fin use for maneuverability	Dumay <i>et al.</i> , [6]
Caudal-peduncle throttling	$\frac{CFd}{CPd}$	CPt	Caudal-propulsion efficiency through reduction of drag	Webb [7]
Aspect ratio of the caudal fin	$\frac{CFd^2}{CFs}$	CFar	Caudal-fin use for propulsion and/or direction	Webb [7]
Fin-surface ratio	$\frac{2 * PFs}{CFs}$	Frt	Main type of propulsion between caudal and pectoral fins	Villéger <i>et al.</i> , [5]
Fin-surface to body-size ratio	$\frac{(2 * PFs) + CFs}{\frac{\pi}{4} * Bw * Bd}$	Fsf	Acceleration and/or maneuverability efficiency	Villéger <i>et al.</i> , [5]
Body mass	$\ln(Mass + 1)$	LogM	Metabolism, endurance and swimming ability	Villéger <i>et al.</i> , [5]

References of Appendix S1

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S1 Table. Geographical coordinates and abiotic variables of the 31 stream reaches analyzed.

Catch.	Site	x	y	% coarse litter	% fine litter	% gravel	% roots	% sand	% clay	pH	Water temp. (°C)	Water cond (µS/cm)	Mean width (cm)	Mean depth (cm)	Distance to nearest large river (km)
1	M01_TN_0900	-59,853	-3,352773	0,33	0,37	0,07	0,07	0,07	0,07	4,39	30,18	49,00	309,67	7,40	20,5
1	M01_TN_2500	-59,839	-3,349004	0,30	0,22	0,11	0,33	0,00	0,04	3,83	27,80	45,00	93,67	4,70	12,7
1	M01_TN_4200	-59,822	-3,345052	0,56	0,22	0,19	0,04	0,00	0,00	4,28	27,77	46,00	364,67	9,30	13,2
1	M01_TS_0000	-59,858	-3,363232	0,85	0,07	0,07	0,00	0,00	0,00	4,26	27,47	40,00	532,67	44,00	16,6
2	M02_TN_0500	-60,332	-3,687772	0,93	0,00	0,07	0,00	0,00	0,00	4,40	25,67	16,00	216,67	17,60	10,9
2	M02_TN_3800	-60,306	-3,671512	0,67	0,00	0,19	0,00	0,00	0,15	4,28	25,84	17,00	253,33	27,50	46,5
2	M02_TN_4200	-60,303	-3,669798	0,74	0,04	0,15	0,00	0,00	0,07	4,45	25,26	18,00	252,33	14,10	47,2
3	M03_TS_0600	-60,736	-4,133673	0,67	0,07	0,04	0,00	0,00	0,22	4,26	26,15	13,00	120,33	13,60	160,1
3	M03_TS_0800	-60,734	-4,135174	0,59	0,22	0,19	0,00	0,00	0,00	4,30	25,67	9,00	173,33	16,20	159,7
3	M03_TS_2200	-60,727	-4,146088	0,74	0,22	0,00	0,04	0,00	0,00	4,53	26,77	11,00	427,33	74,51	158,4
3	M03_TS_2500	-60,726	-4,150065	0,67	0,30	0,04	0,00	0,00	0,00	4,06	27,10	15,00	175,67	20,92	158,1
3	M03_TS_3850	-60,724	-4,159845	0,78	0,19	0,04	0,00	0,00	0,00	4,49	26,31	12,00	181,33	16,00	156
4	M04_TN_0700	-60,948	-4,379451	0,70	0,04	0,00	0,00	0,00	0,26	3,96	25,82	21,00	132,67	21,70	171,8
4	M04_TN_0600	-60,943	-4,383594	0,59	0,19	0,07	0,00	0,00	0,15	4,04	26,03	21,00	232,67	36,79	171,9
4	M04_TN_3060	-60,927	-4,399871	0,41	0,11	0,15	0,00	0,00	0,33	3,61	26,17	28,00	264,00	56,00	170,9
4	M04_TN_3500	-60,925	-4,402961	0,67	0,33	0,00	0,00	0,00	0,00	3,58	26,00	48,00	181,33	20,40	170
5	M05_TN_1350	-61,254	-4,605457	0,63	0,07	0,11	0,11	0,07	0,00	4,54	24,63	18,00	196,67	13,00	228,3
5	M05_TN_1900	-61,261	-4,601374	0,59	0,22	0,07	0,04	0,00	0,07	4,40	24,95	15,00	129,00	9,90	228,2
5	M05_TN_4200	-61,278	-4,588043	0,85	0,00	0,11	0,04	0,00	0,00	4,32	25,24	7,00	136,67	22,20	247
6	M06_TS_0000	-61,573	-4,993704	0,41	0,30	0,22	0,00	0,00	0,07	4,08	25,04	16,00	400,00	72,20	254
6	M06_TS_0500	-61,578	-4,991204	0,67	0,22	0,11	0,00	0,00	0,00	3,84	26,12	15,00	496,67	67,00	254,6
7	M07_TS_0500	-61,933	-5,266952	0,22	0,04	0,22	0,00	0,52	0,00	4,44	24,65	29,00	130,00	17,40	316,2
7	M07_TS_1100	-61,937	-5,263238	0,37	0,07	0,07	0,04	0,44	0,00	4,38	24,46	10,00	306,67	42,40	316,6
7	M07_TS_2600	-61,946	-5,252874	0,26	0,15	0,15	0,07	0,19	0,19	4,20	25,09	13,00	386,67	48,90	317,9

Catch.	Site	x	y	% coarse litter	% fine litter	% gravel	% roots	% sand	% clay	pH	Water temp. (°C)	Water cond (µS/cm)	Mean width (cm)	Mean depth (cm)	Distance to nearest large river (km)
7	M07_TS_4500	-61,958	-5,241985	0,22	0,22	0,26	0,00	0,30	0,00	4,10	24,91	12,00	356,67	39,50	319,5
8	M08_TS_1350	-62,186	-5,632888	0,78	0,11	0,11	0,00	0,00	0,00	4,45	24,62	13,00	121,67	10,90	446,3
8	M08_TS_2260	-62,18	-5,638352	0,41	0,22	0,30	0,07	0,00	0,00	4,33	25,02	19,00	436,00	53,70	447,5
8	M08_TS_3770	-62,167	-5,645023	0,48	0,33	0,15	0,04	0,00	0,00	3,97	25,00	27,00	536,67	32,70	449,1
9	M9_TN_1000	-63,121	-7,205871	0,44	0,44	0,00	0,04	0,00	0,07	3,80	24,52	9,00	432,00	44,00	30,2
9	M9_TN_2000	-63,113	-7,209969	0,33	0,48	0,11	0,07	0,00	0,00	3,71	24,96	7,00	168,33	16,90	26,3
9	M9_TN_2800	-63,105	-7,212862	0,30	0,44	0,04	0,00	0,04	0,19	2,80	24,42	10,00	224,67	25,70	25,9

S2 Table. List of fish species caught along the Purus and Madeira River interfluvium and their functional traits. More details about functional-trait calculations can be found in S1 text. LogM = log (body mass+1); Osh = Oral-gape shape; Ops = Oral-gape position; Edst = Eye size; Eps = Eye position; Bsh = Body transversal shape; Bsf = Body transversal surface; PFps = Pectoral-fin position; PFar = Aspect ratio of the pectoral fin; CPt = Caudal-peduncle throttling; Frt = Fin surface ratio; Fsf = Fin-surface to body-size ratio; Cfar = Aspect ratio of the caudal fin. The maximum lengths were taken from fishbase website ().

Order	Family	Species	specie code	Occur. Freq.	max. length (mm)	logM	Osh	Ops	Edst	Eps	Bsh	Bsf	PFps	PFar	CPt	CFar	Frt	Fsf
Beloniformes	Belonidae	<i>Belonion apodion</i>	2	3,2%	50	2,27	0,92	0,20	0,15	0,84	2,14	2,23	0,50	3,45	0,00	0,00	0,00	0,85
		<i>Potamorhaphis eigenmanni</i>	3	3,2%	228	1,26	4,32	0,57	0,73	0,53	1,03	3,17	0,67	6,70	1,68	0,39	1,08	2,25
Characiformes	Acestrorhynchidae	<i>Acestrorhynchus falcatus</i>	1	3,2%	276	3,38	2,00	0,62	0,50	0,71	1,89	1,73	0,15	3,81	3,57	2,78	0,56	1,89
		<i>Gnathocharax steindachneri</i>	11	9,6%	50	0,28	2,45	0,82	0,67	0,64	2,04	12,95	0,35	4,19	2,53	1,34	1,87	2,62

Order	Family	Species	specie code	Occur. Freq.	max. length (mm)	logM	Osh	Ops	Edst	Eps	Bsh	Bsf	PFps	PFar	CPT	CFar	Frnt	Fsf
	Characidae	<i>Amazonaspinther dalmata</i>	8	16,1%	21	0,05	1,30	0,34	0,67	0,61	1,73	46,10	0,20	5,23	2,29	1,49	0,24	1,72
		<i>Axelrodia stigmatias</i>	9	9,6%	22	0,12	1,96	0,46	0,70	0,56	1,88	21,80	0,12	6,40	2,31	1,19	0,24	1,68
		<i>Bario steindachneri</i>	10	3,2%	115	2,83	1,18	0,67	0,43	0,71	2,19	2,08	0,14	4,87	2,31	2,21	0,47	0,92
		<i>Hemigrammus bellottii</i>	14	35,4%	31	0,40	1,52	0,56	0,67	0,62	2,24	7,81	0,13	7,12	2,62	1,96	0,32	1,59
		<i>Hemigrammus hyanuary</i>	16	6,4%	35	0,24	1,36	0,55	0,63	0,60	2,26	13,93	0,11	6,51	2,54	1,69	0,35	1,58
		<i>Hemigrammus melanochrous</i>	18	51,6%	33	0,20	1,67	0,49	0,63	0,59	2,14	16,01	0,12	4,98	2,83	1,96	0,34	1,66
		<i>Hemigrammus ocellifer</i>	19	29,0%	36	0,41	1,66	0,58	0,61	0,60	2,95	8,43	0,15	7,51	3,10	2,12	0,30	1,63
		<i>Hemigrammus pretoensis</i>	20	3,2%	51	1,49	1,62	0,60	0,49	0,67	2,82	3,27	0,10	3,94	2,66	1,98	0,48	1,73
		<i>Hemigrammus schmardae</i>	21	3,2%	35	0,23	1,78	0,56	0,66	0,56	2,05	13,48	0,11	4,61	3,22	2,10	0,31	1,62
		<i>Hemigrammus sp.</i>	12	3,2%	25	0,34	1,73	0,57	0,63	0,60	2,23	14,44	0,11	6,26	2,80	1,76	0,33	1,48
		<i>Hemigrammus unilineatus</i>	23	3,2%	29	0,34	1,73	0,57	0,63	0,60	2,23	14,44	0,10	6,25	2,78	1,76	0,33	1,48
		<i>Hyphessobrycon agulha</i>	13	9,6%	42	0,74	1,76	0,53	0,64	0,59	2,16	5,41	0,10	5,89	3,46	2,15	0,36	1,80
		<i>Hyphessobrycon bentosi</i>	15	3,2%	32	0,07	1,85	0,68	0,67	0,61	2,27	41,07	0,12	5,80	2,46	1,45	0,38	1,12
		<i>Hyphessobrycon sp.1</i>	17	12,9%	43	0,34	1,73	0,57	0,63	0,60	2,23	14,44	0,10	6,25	2,78	1,76	0,33	1,48
		<i>Hyphessobrycon sp.2</i>	24	35,4%	33	0,34	1,73	0,57	0,63	0,60	2,23	14,43	0,10	6,25	2,78	1,76	0,32	1,48
		<i>Hyphessobrycon sweglesi</i>	22	3,2%	32	0,34	1,73	0,57	0,63	0,60	2,23	14,44	0,11	6,26	2,80	1,76	0,33	1,48
		<i>Moenkhausia aff. lepidura</i>	30	3,2%	59	0,85	1,67	0,56	0,63	0,63	2,28	4,93	0,13	4,72	2,79	2,40	0,49	1,84
		<i>Moenkhausia lepidura</i>	27	3,2%	88	0,85	1,67	0,56	0,63	0,63	2,28	4,93	0,13	4,72	2,79	2,40	0,49	1,84

Order	Family	Species	specie code	Occur. Freq.	max. length (mm)	logM	Osh	Ops	Edst	Eps	Bsh	Bsf	PFps	PFar	Cpt	CFar	Frnt	Fsf
		<i>Moenkhausia mikia</i>	28	3,2%	78	2,22	1,40	0,64	0,53	0,67	2,67	2,49	0,16	4,68	2,85	2,48	0,48	1,30
		<i>Moenkhausia oligolepis</i>	29	6,4%	81	2,23	1,40	0,64	0,53	0,70	2,67	2,49	0,16	4,68	2,86	2,49	0,49	1,30
		<i>Oxybrycon</i> sp.	31	3,2%	21	0,52	2,43	0,63	0,55	0,63	2,58	7,15	0,14	5,04	2,40	1,38	0,34	1,46
		<i>Parapristella</i> sp.	33	3,2%	50	0,27	1,95	0,59	0,64	0,64	2,05	12,51	0,13	4,56	3,14	1,89	0,27	2,11
		<i>Priocharax ariel</i>	32	6,4%	16	0,07	2,05	0,52	0,62	0,61	2,36	31,49	0,27	2,24	2,15	0,92	0,55	2,22
		<i>Tytocharax madeirae</i>	34	6,4%	19	0,07	1,77	0,68	0,57	0,60	2,26	35,71	0,13	4,76	1,96	1,34	0,21	2,20
		<i>Xenobrycon polyancistrus</i>	35	3,2%	14	0,07	1,78	0,68	0,58	0,60	2,26	35,72	0,14	4,77	1,98	1,34	0,21	2,20
	Crenuchidae	<i>Ammocryptochara x elegans</i>	46	6,4%	49	0,22	1,34	0,26	0,69	0,62	1,55	12,40	0,12	3,11	2,05	1,13	0,76	3,42
		<i>Crenuchus spilurus</i>	47	61,2%	39	0,66	1,84	0,48	0,54	0,65	2,14	6,10	0,15	4,69	2,15	1,63	0,28	1,63
		<i>Elachocharax pulcher</i>	48	9,6%	23	0,07	1,46	0,41	0,58	0,60	1,94	36,97	0,13	8,15	1,41	0,87	0,40	2,63
		<i>Microcharacidium gnomus</i>	49	16,1%	15	0,08	1,40	0,41	0,56	0,66	1,79	28,14	0,13	9,08	1,32	0,80	0,55	2,04
		<i>Microcharacidium eleotrioides</i>	50	6,4%	19	0,09	1,27	0,31	0,57	0,66	1,43	24,67	0,12	5,67	1,40	0,87	0,62	3,06
		<i>Microcharacidium weitzmani</i>	51	16,1%	12	0,07	1,39	0,42	0,60	0,63	1,72	30,39	0,09	5,59	1,30	0,62	0,60	3,22
		<i>Odonthocharacidium aphanes</i>	52	19,3%	14	0,04	1,28	0,32	0,73	0,54	1,67	49,14	0,09	6,70	2,11	1,18	0,29	1,49
	Erythrinidae	<i>Erythrinus erythrinus</i>	53	41,0%	231	2,34	1,10	0,52	0,52	0,67	1,21	2,32	0,22	2,33	1,31	1,08	0,64	2,19
		<i>Hoplerythrinus unitaenitatus</i>	55	16,1%	300	3,40	1,04	0,51	0,45	0,73	1,33	1,80	0,18	2,55	1,48	1,07	0,64	1,80
		<i>Hoplías malabaricus</i>	54	45,1%	500	3,78	1,32	0,52	0,49	0,76	1,44	1,67	0,19	2,48	1,45	1,17	0,68	2,05
	Gasteropelecidae	<i>Carnegiella marthae</i>	56	3,2%	28	0,23	1,62	0,86	0,57	0,63	4,02	14,18	0,68	5,38	2,62	1,19	1,56	2,73
		<i>Carnegiella strigata</i>	57	45,1%	35	0,64	1,41	0,87	0,53	0,70	3,65	6,52	0,71	4,83	3,16	1,63	1,78	2,60

Order	Family	Species	specie code	Occur. Freq.	max. length (mm)	logM	Osh	Ops	Edst	Eps	Bsh	Bsf	PFps	PFar	Cpt	CFar	Frnt	Fsf
		<i>Gasteropelecus sternicla</i>	58	3,2%	37	0,95	1,44	0,88	0,48	0,68	3,94	4,64	0,70	5,49	3,18	1,61	1,82	2,40
	Iguanodectidae	<i>Iguanodectes geisleri</i>	25	16,1%	55	0,77	1,29	0,48	0,73	0,57	1,50	5,04	0,12	5,48	3,69	1,78	0,31	1,93
	Iguanodectidae	<i>Iguanodectes purusi</i>	26	12,9%	75	1,28	1,16	0,53	0,70	0,60	1,75	3,35	0,14	6,17	2,89	1,50	0,35	1,75
	Lebiasinidae	<i>Copeina guttata</i>	76	9,6%	76	0,35	1,68	0,79	0,68	0,60	1,85	9,29	0,20	5,67	1,77	0,76	0,37	3,96
		<i>Copella nattereri</i>	75	6,4%	42	0,21	1,56	0,74	0,76	0,57	1,84	14,51	0,23	4,96	1,80	0,94	0,38	2,50
		<i>Copella callolepis</i>	77	77,4%	37	0,37	1,43	0,77	0,74	0,58	2,00	8,55	0,21	5,18	1,73	0,90	0,39	2,88
		<i>Nannostomus digrammus</i>	79	3,2%	26	0,08	1,14	0,49	0,78	0,58	1,78	28,96	0,24	5,57	1,87	0,86	0,21	2,35
		<i>Nannostomus eques</i>	80	6,4%	27	0,25	1,33	0,42	0,81	0,53	1,72	11,90	0,18	6,50	2,27	1,44	0,26	2,03
		<i>Nannostomus marginatus</i>	81	22,5%	35	0,15	1,12	0,55	0,75	0,54	2,06	18,08	0,21	5,16	1,90	1,28	0,30	2,18
		<i>Nannostomus unifasciatus</i>	78	3,2%	32	0,25	1,33	0,42	0,81	0,53	1,72	11,90	0,18	6,50	2,27	1,44	0,26	2,03
		<i>Pyrrhulina lugubris</i>	82	48,3%	50	0,89	1,32	0,77	0,71	0,63	1,76	4,80	0,21	4,05	1,71	1,00	0,46	2,69
		<i>Pyrrhulina semifasciata</i>	83	3,2%	40	0,33	1,75	0,74	0,74	0,57	2,11	11,55	0,20	4,76	1,67	0,91	0,46	3,11
		<i>Pyrrhulina zigzag</i>	84	6,4%	35	0,31	1,53	0,77	0,73	0,60	1,90	10,28	0,22	4,54	1,61	0,91	0,48	2,53
Cyprinodontiformes	Rivulidae	<i>Anablepsoides atratus</i>	91	6,4%	40	0,35	0,72	0,70	0,62	0,58	1,12	9,62	0,44	2,90	1,53	0,78	0,64	3,13
		<i>Anablepsoides micropus</i>	93	16,1%	80	0,65	0,70	0,74	0,69	0,61	1,16	6,49	0,45	2,85	1,85	0,94	0,45	3,51
		<i>Anablepsoides ornatus</i>	94	6,4%	21	0,09	0,63	0,64	0,71	0,55	0,91	27,77	0,54	3,39	1,40	0,55	0,61	3,08
		<i>Moema sp.</i>	89	6,4%	120	0,49	0,84	0,78	0,70	0,58	1,32	7,84	0,41	3,24	1,51	0,73	0,70	3,48
		<i>Laimosemion kirovskyi</i>	92	6,4%	25	0,08	0,66	0,80	0,67	0,64	1,05	30,36	0,45	2,79	1,29	0,54	0,56	2,88
		<i>Pterolebias longipinnis</i>	90	3,2%	120	0,35	0,72	0,70	0,61	0,57	1,12	9,62	0,43	2,89	1,52	0,77	0,64	3,10
Gymnotiformes	Gymnotidae	<i>Gymnotus carapo</i>	59	12,9%	302	2,09	0,73	0,76	0,21	0,72	2,04	2,59	0,39	2,34	0,00	0,00	0,00	0,46

Order	Family	Species	specie code	Occur. Freq.	max. length (mm)	logM	Osh	Ops	Edst	Eps	Bsh	Bsf	PFps	PFar	Cpt	CFar	Frnt	Fsf
		<i>Gymnotus coropinae</i>	60	25,0%	160	1,15	0,59	0,77	0,24	0,71	1,83	3,54	0,37	2,17	0,00	0,00	0,00	0,49
		<i>Gymnotus curupira</i>	61	16,1%	239	1,14	0,59	0,77	0,23	0,71	1,83	3,54	0,37	2,17	0,00	0,00	0,00	0,49
	Hypopomidae	<i>Brachyhypopomus batesi</i>	67	3,2%	170	1,55	0,76	0,38	0,24	0,81	2,14	3,28	0,39	2,06	0,00	0,00	0,00	0,51
		<i>Brachyhypopomus beebei</i>	68	22,5%	250	1,52	0,76	0,38	0,21	0,81	2,14	3,27	0,38	2,06	0,00	0,00	0,00	0,51
		<i>Brachyhypopomus brevirostris</i>	69	3,2%	347	1,47	0,71	0,42	0,26	0,75	2,36	3,10	0,40	2,74	0,00	0,00	0,00	0,71
		<i>Brachyhypopomus hamiltoni</i>	70	12,9%	208	1,52	0,75	0,37	0,21	0,80	2,14	3,27	0,38	2,06	0,00	0,00	0,00	0,51
		<i>Brachyhypopomus sullivanii</i>	71	16,1%	150	1,52	0,76	0,38	0,21	0,81	2,14	3,28	0,38	2,06	0,00	0,00	0,00	0,51
		<i>Microsternarchus bilineatus</i>	74	3,2%	120	0,56	0,98	0,35	0,25	0,72	2,13	6,14	0,32	3,27	0,00	0,00	0,00	0,43
	Rhamphichthyidae	<i>Gymnorhamphicht hys rondoni</i>	88	6,4%	250	0,55	1,42	0,36	0,23	0,81	2,19	7,06	0,31	3,82	0,00	0,00	0,00	0,98
		<i>Hypopygus cryptogenes</i>	72	3,2%	116	0,50	0,96	0,30	0,22	0,69	2,25	7,22	0,45	2,10	0,00	0,00	0,00	0,63
		<i>Hypopygus lepturus</i>	73	22,5%	116	0,50	0,96	0,30	0,22	0,70	2,25	7,22	0,45	2,10	0,00	0,00	0,00	0,63
Cichliformes	Cichlidae	<i>Aequidens pallidus</i>	40	6,4%	143	1,97	1,15	0,34	0,43	0,69	2,60	2,91	0,38	3,16	1,47	0,82	1,10	2,20
		<i>Aequidens tetramerus</i>	39	29,3%	169	3,47	1,03	0,33	0,40	0,71	2,22	1,92	0,37	3,18	1,50	0,97	1,37	2,01
		<i>Aequidens sp.</i>	41	9,6%	162	1,93	1,12	0,34	0,49	0,68	2,57	2,95	0,36	3,80	1,61	0,85	1,03	2,36
		<i>Apistogramma agassizii</i>	36	67,7%	33	0,50	1,27	0,39	0,53	0,71	2,09	7,64	0,37	3,06	1,39	0,71	0,75	2,73
		<i>Apistogramma gephyra</i>	37	3,2%	33	0,392	1,128	0,382	0,55	0,702	2,07	9,821	0,377	3,074	1,14	0,561	0,976	2,23
		<i>Apistogramma pulchra</i>	38	3,2%	32	0,34	1,17	0,37	0,53	0,71	2,10	11,31	0,39	3,16	1,45	0,81	0,81	2,33
		<i>Crenicichla inpa</i>	42	6,4%	168	2,12	1,32	0,43	0,65	0,67	1,74	2,48	0,49	2,36	1,67	0,92	1,10	3,36
		<i>Laetacara cf. dorsigera</i>	43	3,2%	60	1,89	1,09	0,33	0,51	0,71	2,09	2,90	0,34	2,74	1,74	1,10	0,78	2,41

Order	Family	Species	specie code	Occur. Freq.	max. length (mm)	logM	Osh	Ops	Edst	Eps	Bsh	Bsf	PFps	PFar	Cpt	CFar	Frnt	Fsf
		<i>Laetacara cf. thayeri</i>	44	3,2%	120	1,88	1,09	0,33	0,51	0,71	2,09	2,90	0,34	2,74	1,74	1,10	0,77	2,40
		<i>Laetacara sp.</i>	45	6,4%	60	1,88	1,08	0,32	0,50	0,70	2,06	2,90	0,33	2,73	1,73	1,09	0,77	2,40
Siluriformes	Cetopsidae	<i>Helogenes marmoratus</i>	7	12,9%	51	1,24	0,71	0,39	0,20	0,81	1,96	3,67	0,48	2,73	1,83	1,27	0,81	3,26
	Callichthyidae	<i>Callichthys callichthys</i>	5	38,7%	125	1,13	0,65	0,32	0,20	0,81	0,93	5,04	0,22	2,05	1,74	1,19	0,59	2,66
		<i>Corydoras bilineatus</i>	4	6,4%	40	1,09	0,84	0,10	0,29	0,75	1,75	4,71	0,15	3,65	2,04	1,41	0,69	1,76
		<i>Leptoplosternum beni</i>	6	9,6%	50	2,26	0,69	0,31	0,30	0,73	1,18	3,19	0,16	2,49	1,67	1,06	0,61	2,74
	Loricariidae	<i>Acestridium discus</i>	85	6,4%	67	0,31	1,10	0,00	0,37	0,72	0,90	9,59	0,25	2,52	7,48	1,71	1,84	2,52
		<i>Hypostomus sp.</i>	86	9,6%	250	2,00	0,96	0,00	0,35	0,85	0,93	3,05	0,09	3,23	3,94	1,55	0,85	2,71
		<i>Pterygoplichthys pardalis</i>	87	6,4%	490	2,00	0,98	0,00	0,35	0,85	0,93	3,05	0,10	3,23	3,94	1,55	0,85	2,71
	Heptapteridae	<i>Gladioglanis conquistador</i>	62	12,9%	31	0,11	0,52	0,40	0,35	0,85	0,78	22,97	0,47	3,27	1,33	0,36	0,45	2,33
		<i>Nemuroglanis cf. furcatus</i>	63	3,2%	47	0,09	0,65	0,46	0,35	0,92	0,84	28,18	0,38	3,59	1,53	0,62	0,37	3,42
		<i>Pimelodella boliviana</i>	64	3,2%	103	0,94	0,75	0,28	0,48	0,82	1,28	4,76	0,26	2,84	2,54	1,09	0,63	3,15
		<i>Rhamdia quelen</i>	65	22,5%	255	1,83	0,78	0,26	0,39	0,89	1,18	3,04	0,32	2,80	1,98	1,18	0,50	2,47
		<i>Rhamdia muelleri</i>	66	3,2%	230	2,65	0,75	0,32	0,42	0,88	1,23	2,25	0,32	2,62	2,01	1,21	0,50	2,41
	Trichomycteridae	<i>Ituglanis amazonicus</i>	97	9,6%	79	0,35	0,63	0,37	0,23	0,94	1,18	9,33	0,54	2,90	1,31	0,70	0,28	2,47
		<i>Tridens sp.</i>	98	3,2%	16	0,03	0,83	0,23	0,29	0,92	1,18	64,23	0,42	4,70	1,39	0,84	0,40	1,64
Synbranchiformes	Synbranchidae	<i>Synbranchus madeirae</i>	95	12,9%	493	1,38	1,17	0,38	0,33	0,75	1,14	2,67	0,00	0,00	0,00	0,00	0,00	0,00
		<i>Synbranchus sp.</i>	96	16,1%	335	1,17	1,20	0,40	0,39	0,83	1,07	2,90	0,00	0,00	0,00	0,00	0,00	0,00

ARTIGO 3

Interannual variability in fish assemblages composition in highly dynamics streams of Central Amazonia

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Manuscrito em elaboração para a *Freshwater biology*

Abstract

Biological assemblages are dynamic entities and drought is one of the main natural disturbances that periodically alters the structure of biological assemblages. In systems that cease to flow or dry at some point along their course, the assemblages' stability over time depends on the resistance and resilience of the species, coupled with favorable conditions that facilitate the arrival of individuals to newly formed habitats. In this study we aimed to characterize the interannual variations of fish assemblages of intermittent streams in Central Amazonia and to evaluate the role of local conditions and connectivity to the floodplain in the stability of the assemblages. We sampled fish assemblages in 11 streams reaches during the wet season of 2015 and 2016. We collected 3,216 individuals from 60 species, 39 genera, 18 families e 7 orders and eight species (*Crenuchus spilurus*, *Erythrinus eryrthinus*, *Hoplias malabaricus*, *Copella callolepis*, *Pyrrhulina laeta*, *Gymnotus coropinae*, *Brachyhypopomus hamiltoni* e *Apistogramma agassizii*) occurred in at least 50% of the sample occasions. There was extensive species replacement between years and 15 species were captured exclusively in 2015, 13 caught only in 2016. The permutation analysis detected significant changes in the composition of the assemblages between years for quantitative and qualitative data but ordination analysis suggests a convergent trajectory of change for most of the assemblages. We detected a negative effect of the floodplain connectivity in relation of the trajectory length, indicating that streams with greater influence of the floodplain were those with more stable composition between years. Our results show that there is a strong interannual variability in the composition of fish assemblages in intermittent streams in Central Amazonia and proximity to the floodplain should represent an advantage for species persistence over time.

Key words: Intermittent systems; Stream-fish ecology; Interannual variability; Trajectory analysis; Central Amazonia.

Introduction

Biological communities are dynamic entities that experience varying degrees of stability, according to the environmental variability they are exposed to (Winemiller, 1996; Oberdorff, Hugueny & Vigneron, 2001). In aquatic environments, extreme variations in water flow, such as drought regimes, are one of the main natural disturbances that periodically alters the structure of biological assemblages ; Taylor & Warren, 2008). The assemblages' stability over time in dynamic environments (i.e. the ability to return to an initial state prior to the next disturbance) depends on the resistance and resilience of the species, coupled with favorable conditions that facilitate the arrival of individuals to newly formed habitats (Benda et al., 2004; .

Intermittent streams (i.e. flowing waters that cease to flow and/or dry at some point along their course) are highly disturbed ecosystems (Datry, Bonada & Boulton, 2017). Stream drying is stressful for fish species and can cause heavy and widespread mortality and large oscillations in the abundance of species, which can lead to local extinctions and changes in the structure and functioning of ecosystems (Lake, 2000; Bonada et al., 2007; Davey & Kelly, 2007). Most fish need to migrate to areas with adequate conditions and proximity to perennial and hydrologically more stable environments such as downstreams habitats or pools (Davey & Kelly, 2007; Taylor & Warren, 2008; Datry *et al.*, 2016). In thus sense, the assemblages' stability can be very dependent on the permeability of the landscape and connectivity with refuge areas, which will facilitate the colonization dynamics and ensure the survival of the species during the drought (Labbe & Fausch, 2000; Davey & Kelly, 2007; Pusey *et al.*, 2018)

Fish assemblages of intermittent streams are generally composed of a subset of species from perennial streams to which they are connected, since extreme environmental conditions select species that bear adaptations to survive to harsh conditions and/or with high resilience (Perkin & Gido, 2012; Pusey et al., 2018). The strong environmental filter imposed by the environment, especially in arid

regions, makes the assemblages' structure generally quite predictable, since many species avoid intermittent environments (Pusey et al., 2018). Pusey *et al.* (2018) found similarity in the structure of the assemblages at the end of the wet season over the 7-year, and suggest dispersal processes to be themselves predictable or that the processes that structure fish assemblages after dispersal has occurred result in the formation of predictable assemblage structure. However, predictability may not be held in systems with high species diversity and large density of perennial networks, such as intermittent streams on ombrophilous tropical forests. In these environments, high richness creates strong substitution patterns in space and can generate structuring patterns often associated with stochastic processes (Cilleros *et al.*, 2016; Stegmann *et al.*, 2019). How the substitution of species in hyperdiverse environments operates on temporal scales and affects the stability of the assemblages is still poorly understood.

Studies about seasonal changes in Amazonian streams are so far limited to perennial environments, which, despite undergoing expansion and contraction processes according to rainfall, remain connected to downstream drainage throughout the year. The abiotic and structural variations of these streams between the dry and wet seasons are low accentuated and thus changes in the composition of fish assemblages are not always detectable (Buhrnheim & Cox Fernandes, 2001). Some studies have reported alternations of habitat occupation by the streams fishes according to the increased flow and overflow of the mainstream in the wet season, but a strong tendency to return to the initial conditions, when the flow regresses (Pazin *et al.*, 2006; Espírito-Santo *et al.*, 2009). However, in intermittent streams the environmental changes throughout the seasonal cycle are extreme and periodically reset the assemblages, creating discontinuities in time, which can incorporate high stochasticity in the assembly rules.

Understanding and predicting when and how biodiversity might change following disturbance is crucial for effective conservation and management (Dornelas, 2010) specially in the Amazon, where

combined effects of climate change and deforestation are altering precipitation patterns (Gloor *et al.*, 2013). In this study we aimed to characterize the interannual variations of fish assemblages of intermittent streams in Central Amazonia and to evaluate the role of local conditions and connectivity to the floodplain in the stability of the assemblages. Our hypothesis is that the disturbance caused by the dry season and the constant recolonization of these environments incorporates a lot of stochasticity in the recruitment of the species and generates oscillations of composition over time. We also hypothesize that the connectivity with the floodplain facilitates the colonization of these environments and acts as refuge during the drought events, favoring the permanence of the species between years.

Methods

Study Area

The Purus-Madeira interfluve is covered by dense rainforest with mean annual precipitation varying from 2,000 to 2,400 mm . The region is located in a predominantly flat to gently undulating, relatively low-lying lands with fine sandy to silty sediments, the Late Pleistocene unstable formation named for Sombroek (2000) as “loamy plains”. The water-table is shallow, within 7 m of the surface throughout the year in most of the region but some areas are subject to shallow flooding (~50 cm) when the water-table reaches the highest levels , which results in poorly drained soils (Sombroek, 2000). The low permeability of the soil combined with a shallow water-table inhibits deep infiltration and consequently decreases the system storage capacity, creating a dynamic hydrological cycle. The water-table is rapidly saturated during the wet season and large areas are waterlogged, but the shallow water-table cannot supply the stream flow for a few consecutive dry months during the dry season, forcing some streams to dry.

Sampling was carried out in 11 streams (50-m long reaches in 1st to 3rd order streams) from three catchments along the Purus-Madeira interfluve, Amazonas State, Brazil (figure 1). The streams of

catchment 1 drain into the Amazon River while catchments 2 and 3 flow into the Tupana River, a tributary of the Madeira River. These streams dry when the rain stops, or persist as isolated pools along the stream bed. We sampled during the rainy season in March 2016, and between April and May 2017, in similar times in relation to the rainfall cycle (Figure 2). During this period, the water level remained stable for months, allowing recolonization after the dry season. All stream segments sampled are permanent sampling plots of the Research Program in Biodiversity (PPBio) field-site network (<http://ppbio.inpa.gov.br/sitios/br319>).

Sampling

Stream-habitat variables and inundation measurement

In each stream reach, we measured water temperature, electrical conductivity, dissolved oxygen and pH with a YSI Pro 1030® multiparameter probe. We also measured channel width, depth, substrate type and flow velocity in four transects perpendicular to the stream channel, separated from each other by 12.5m. Depth and substrate type were measured in nine equidistant points along each transect across the stream channel. Substrate was classified in one of six categories: sand, clay, trunk (wood with diameter >10 cm), coarse litter (leaves and small branches), fine litter (organic silt) or roots (fine roots from riparian vegetation). Flow velocity was estimated as the average time that a floating object took to travel 1 m, replicated three times. For statistical analyses, we use the average values of channel width, depth, flow velocity and the percentage of each substrate type of each stream reach. See for details of the environmental-sampling protocol.

In order to measure the extent of flooding around each stream reach, we used an JERS-1 L-band radar imager acquired during a high-water period. L-band synthetic aperture radar (SAR) are particularly useful for mapping wetlands because they can reliably detect flooding beneath most vegetation canopies (Hess *et al.*,1990). We calculated the mean value of the pixels in a 1 km buffer around each sampled point (hereafter ‘inundation connectivity’), which represents the mean value of

reflectance captured by the radar in each area. Manipulation of raster and vector data was done using ‘*raster*’ and ‘*sp*’ packages in R software

Fish sampling

In each stream, a 50-m long reach was isolated with block nets (5mm mesh) and fish were caught using seines and hand nets. Fish were collected only during the day and collection effort in each section was standardized by using two collectors over two hours. The specimens were euthanized in clove-oil solution, which decreases fish neurosensory functions by acting upon the nervous systems. The specimens were fixed in 10% formalin and preserved in 70% ethanol. Fish were sorted, counted and identified to species level in the laboratory using dichotomous keys and specialized literature, such as . All collected specimens were deposited in the fish collection of the Instituto Nacional de Pesquisas da Amazônia (INPA).

Statistical analyses

All statistical analyses were carried out using R software (R Development Core Team 2015). Taxonomic richness and abundance of stream-fish assemblages were calculated for each site and then one-way analyses of variance (ANOVA) was used to test for differences between years for each metric. To test for differences among years in the overall assemblage composition, we ran a np-MANOVA for quantitative data (fish abundance) and qualitative data (presence-absence), using the Bray–Curtis index. To standardize the abundance data, the number of individuals of each species was divided by the total number of fish at each sampling site. To summarize the changes in the composition of the assemblages between years we used a principal component analysis (PCoA), for abundance and presence-absence data, using the Bray-Curtis index. To quantify the extension of the variation of each assemblage between years, we calculate the distances between assemblages observed at different sampling times (hereafter "Trajectory Length") in a ordination diagrams using the function '*trajectoryLengths*' developed by for abundance data. To evaluate whether the temporal changes within sites are dominated by gains or by losses of species/individuals, we estimated the species losses and

gains at each site between years, using the function ‘*TBI*’, developed by . To further assess which species differed between years, we used an indicator species analysis (INDVAL) (Dufrêne & Legendre 1997).

To assess whether there were significant changes in local conditions between years, we computed a one-way analysis of variance (ANOVA) between years for each environmental variable measured (pH, conductivity, temperature, dissolved oxygen, substrate-type ratio, flow velocity, stream width and depth). To test whether the interannual changes in assemblages structure were related to environmental changes or connectivity with the floodplain, we used the variables indicated by the analysis of variance as significantly different among years, and retained only their inter-annual differences. We then used the difference in abiotic variables and the inundation connectivity values as fixed effects in a linear mixed-effect model (LMM) in relation to the trajectory length and the species gains and losses. Catchment was included in the model as a random variable to account for the nested design (stream within catchment).

Results

We collected 3,216 individuals from 60 species, 39 genera, 18 families e 7 orders (Table 1). Forty seven species were collected in 2016 and 45 in 2017. Thirty-two species occurred in both years (black bars in figure 3) and eight species (*Crenuchus spilurus*, *Erythrinus erythrinus*, *Hoplias malabaricus*, *Copella callolepis*, *Pyrrhulina laeta*, *Gymnotus coropinae*, *Brachyhyopomus hamiltoni* e *Apistogramma agassizii*) occurred in at least 50% of the sample occasions. Although registered in fewer sampling occasions, *Hemigrammus bellottii* was the most abundant species and accounted for 29% of all individuals collected.

There was extensive species replacement between the two years and 15 species were captured exclusively in 2015, 13 caught only in 2016 (yellow bars in figure 3). The number of species per stream reach was similar between years and ranged from six to 19 in 2015 and from five to 20 in 2016 (one-

way ANOVA; $P=0.8$). More than double the number of specimens were collected in 2015 than in 2016 (2,360 e 856, accordingly). This was mainly due to the high abundance of characid species in one site in 2016. Not all streams had a higher number of specimens in 2016, as indicated by the indices of species loss and gain (figure 4A), and the analysis of variance did not detect significant changes in the number of individuals per stream between years (on-way ANOVA; $P=0.06$).

The ordination analysis using abundance data (figure 4A) showed a convergence in the trajectory of interannual changes, mainly in streams of catchments 2 and 4. This pattern was mainly related to interannual fluctuations in the abundance of some species, as showed by INDVAL results, which indicated that *Callichthys callichthys* ($P=0.005$), *Erythrinus erythrinus* ($P=0.001$) and *Hoplias malabaricus* ($P=0.02$) were significantly more abundant in 2015, while *Apistogramma agassizii* ($P=0.001$), *Gymnotus coropinae* ($P=0.01$), *Microsternarchus bilineatus* ($P=0.002$) and *Hyphessobrycon cf. wosiackii* ($P=0.01$) were significantly more abundant in 2016 (blue bars in figure 3). The interannual variation of fish assemblages was less evident for presence/absence data (figure 4B), but most trajectories point to the same direction. This pattern was corroborated by the permutation analysis, which detected significant changes in the composition of the assemblages between years for both quantitative and qualitative data (Abundance data: $F = 3.8$, $R^2 = 0.162$, $P = 0.001$ and P/A data: $F = 3.7$; $R^2=0.157$; $P=0.001$).

Analysis of variance indicated that only temperature and flow velocity showed significant variation between years (table 2). These variables, however, had no effect on the trajectories of fish assemblages or on the metrics of species gain or species loss (table 3). The LMM model results indicated a significant relationship between the floodplain connectivity and the trajectory length, indicating that streams with greater influence of the floodplain were those with more stable composition between years (figure 5B). In fact, most species recorded in the year 2015 were also recorded in 2016 in streams from catchment 3 (those with the greatest influence of the floodplain), whereas there was a greater variation in composition in the other streams. In addition, there was also a

high gain of new species in the streams closest to the floodplain in 2016 (Figure 5A), corroborated by the LMM results (table 3). The stream reach with less influence of floodplain had the greatest loss of species richness, which decreased from 19 to five species between 2015 and 2016. However, the loss of species was variable among streams and the analysis did not detect any significant relationship with the predictor variables.

Discussion

Our results show that there is a strong interannual variability in the composition of fish assemblages of intermittent streams of Central Amazonia and that changes are not related to local factors, since the environmental conditions of the streams were generally similar in both years. Seasonal variations in flow velocity and temperature, are common in perennial tropical streams due to changes in the frequency of rainfall in the local catchment (Walker, 1995), however its does not result in large variation in fish assemblages, such as those that we found . Despite the short period analyzed, our results provide an indication that the constant reestablishment of populations due to drought events can result in high levels of stochasticity of recruitment and mortality of species.

Stochastic patterns are common in environments with unpredictable hydrological dynamics , while more stable environments or those subject to gradual changes tend to have more deterministic occupation dynamics . Drying of the studied streams is related to predictable seasonal changes in the water level of the major drainage areas, but refuges, such as residual pools in the streams beds, may vary greatly between years according to the climatic conditions and represent important habitats for the local persistence of some fish populations . The proximity to the floodplain should also represent an advantage for the maintenance of species more susceptible to harsh conditions imposed by the drought that need to migrate to more stable environments at the beginning of the dry season. This may explain the higher compositional stability found in assemblages more connected to the floodplain, which in addition to having greater compositional similarity between years, also had the largest increase in

numbers of species and individuals in 2016.

According to Connell and Sousa (1983), persistence and stability are two key characteristics for determining variation in the composition of biological assemblages. Our results show that both persistence and stability of the fish assemblages were low during the period analyzed, since we detected significant differences between the years for both quantitative and qualitative data. The instability that we found, especially in streams less connected to the floodplain, was mainly associated with the substitution of species with low abundances between years while the most dominant varied in the number of individuals but persisted between years. According to , the instability results from strong biotic interactions among temporally persistent core species and stochastic dynamics among infrequent satellite species. Rarity is a key characteristic of tropical assemblages () and causes high composition variability between sites generating substitution patterns even at small geographic scales . Our results show that in highly dynamic environments, the high substitution of species also occurs on temporal scales. The effects of these oscillations on system functioning can be better understood with approaches that integrate information about the functional traits of species.

Dispersal and disturbance are two key ecological processes that shape local and regional diversity patterns , Dodd et al. 2006). In our study, the assemblage stability was mainly determined by the connection with the floodplain, suggesting that dispersion and connectivity between headwater systems and floodplains are fundamental for the maintenance of the recolonization dynamics of these environments. The fact that streams farther from the floodplain show greater oscillation of species losses and gains may also suggest that these assemblages have slower occupation dynamics, and thus exhibit more intermediate states of composition, while assemblages more connected to the floodplains recover more quickly (Fausch *et al.*, 2002, Davey & Kelly 2007). More sampling considering different moments in the colonization process is needed to determine whether these assemblages tend to converge to the same state at the end of the rainy season and the role of priority effects in interannual composition variability.

Fish assemblages in intermittent streams generally have low richness and are composed primarily of generalist species or species with adaptations to survive dry conditions ; . However, the richness found in our study was similar and in some cases even larger than that normally found in perennial streams in Central Amazonia (; Mendonça *et al.*, 2005). This may be due to the immense network of perennial drainage of the Amazonian systems, which act as refuges and should dampen the possible environmental constraints imposed by drought events. Also, many Amazonian species have strategies to survive in low-water periods, such as tolerance to hypoxia and high temperature , which allows many species to survive in systems with large annual water-level oscillations. Most of the species listed by the INDVAL results as significantly more abundant in one of the sampled years are species with adaptations to withstand low oxygen periods and are abundant in the flood zones of large rivers . In most cases, these species were present in high abundance and in juvenile stages, which indicates a strong relationship between floodplain recruitment events and these environments and also is indicative that these streams can serve as nursery areas for juvenile forms of larger species that do not establish populations in small streams.

The fact that different drainages separated by more than 90 km had very similar trajectories of change is also an indication that the dynamics of occupation of these environments are highly influenced by factors external to the local catchment, such as the floodplains of large rivers. Flooded areas can acts as keystone sites and has the ability to act as a propagule source during dispersal events, thus controlling source–sink dynamics . More studies are necessary to elucidate the role of connectivity between intermittent drainages and the floodplain in recruiting and maintaining Amazonian fish diversity.

Understanding how drought events change species persistence over time is critical to predict possible impacts of climate change on biodiversity since in recent decades more streams and rivers are drying (Acuña *et al.*, 2014). Our study shows a great dynamism in assemblages composition over time but the connectivity between habitats is fundamental to ensure species persistence. Management and

conservation strategies should aim to maintain movement opportunities at large spatial scales to preserve population resilience (Marshall et al. 2016). This aspects needs to be incorporated in territorial planning of this region, that may be quite fragmented in the coming years due to infrastructure constructions . Long-term studies also are needed to improve our ability to predict the direction of assemblages changes over time and to have more robust information about the hydrological dynamics and occurrence area of intermittent systems in Central Amazon.

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TABELAS

Table 1. Abundance fish species in each stream sampled between 2016 (round 1) and 2017 (round 2). “CATCHM” represent the three catchments analyzed and S1 to S11 represents the streams reaches sampled.

		Round 1											Round 2												
		CATCHM. 1			CATCHM. 2				CATCHM.3					CATCHM. 1			CATCHM. 2				CATCHM.3				
		S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	total	
Characiformes																									
Curimatidae	<i>Curimatopsis crypticus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	5	0	0	0	0	42	
Crenucidae	<i>Crenuchus spilurus</i>	3	2	2	7	5	0	10	0	0	0	0	0	15	12	7	10	8	0	3	0	8	0	92	
	<i>Elachocharax pulcher</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	6	0	0	0	0	9	
	<i>Microcharacidium gnomus</i>	0	1	1	0	0	0	0	5	0	0	1	0	0	0	4	0	0	0	0	0	0	0	12	
	<i>Odonthocharax um aphanes</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	5	
Gasteropelecidae	<i>Carnegiella marthae</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
	<i>Carnegiella strigata</i>	3	5	5	0	3	0	0	0	1	0	0	0	1	2	0	0	7	2	0	0	0	0	29	
Characidae	<i>Axelroidea stigmatias</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	0	0	0	0	0	6	
	<i>Bario steindachneri</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
	<i>Byconella pallidifrons</i>	15	0	3	1	0	0	0	0	6	0	0	0	0	0	11	0	0	0	0	0	0	0	36	
	<i>Gnathocharax steindachneri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	
	<i>Hemigrammus aff. prata</i>	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	
	<i>Hemigrammus bellottii</i>	8	0	0	0	0	46	0	0	0	0	0	0	38	0	0	63	468	83	0	0	0	0	706	
	<i>Hemigrammus melanochrous</i>	0	2	0	0	0	0	0	2	0	7	0	0	84	103	20	0	0	0	9	0	21	0	248	
	<i>Hemigrammus ocellifer</i>	0	0	1	4	0	0	4	0	0	0	0	0	3	0	0	4	86	13	0	0	3	0	118	
	<i>Hemigrammus vorderwinkleri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	70	2	0	0	0	0	72	
	<i>Hyphessobrycon cf. wosiackii</i>	0	0	0	0	0	0	0	0	0	1	0	2	147	140	49	0	0	0	24	0	22	0	385	

		Round 1										Round 2										
		CATCHM. 1			CATCHM. 2			CATCHM.3				CATCHM. 1			CATCHM. 2			CATCHM.3				
	<i>Moenkhausia oligolepis</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Moenkhausia sp.</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Tyttocharax madeirae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3
	<i>Priocharax ariel</i>	0	0	0	0	0	3	0	0	0	14	0	0	0	0	0	17	0	14	0	0	48
Acestrorhynchidae	<i>Acestrorhynchus falcatus</i>	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	5
	<i>Erythrinus erythrinus</i>	33	26	42	2	2	0	1	14	0	11	5	0	1	0	1	0	0	0	0	0	138
Erythrinidae	<i>Hoplerythrinus unitaeniatus</i>	6	5	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	13
	<i>Hoplias malabaricus</i>	5	15	29	3	4	0	1	4	0	0	1	0	0	0	2	0	1	2	0	0	68
Lebiasinidae	<i>Copella callolepis</i>	2	2	5	8	7	0	46	1	0	0	0	0	14	0	9	85	89	20	0	0	294
	<i>Nannostomus unifasciatus</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	4
	<i>Nannostomus digrammus</i>	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	15	0	0	0	0	23
	<i>Nannostomus emarginatus</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Nannostomus eques</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Nannostomus trifasciatus</i>	2	1	1	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	14
	<i>Pirrhulina laeta</i>	2	5	0	10	3	0	0	0	0	14	3	2	4	7	0	0	0	0	0	16	67
	<i>Pyrrhulina zigzag</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
	<i>Pyrrhulina semifasciata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	10
Siluriformes																						
Cetopsidae	<i>Helogenes marmoratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	1	0	0	7
Trichomycteridae	<i>Ituglanis gracillior</i>	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Callichthyidae	<i>Callichthys callichthys</i>	8	18	25	0	1	0	0	0	3	5	1	0	0	0	0	0	0	0	0	0	61
	<i>Megalechis picta</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	3
Heptapteridae	<i>Gladioglanis conquistador</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	5	0	0	0	12	0	0	24

		Round 1											Round 2											
		CATCHM. 1			CATCHM. 2				CATCHM.3					CATCHM. 1			CATCHM. 2				CATCHM.3			
	<i>Rhamdia cf. quelen</i>	17	0	0	0	0	0	0	10	2	15	16	0	0	0	0	3	0	0	8	1	1	0	73
Gymnotiformes																								
Gymnotidae	<i>Gymnotus carapo</i>	2	0	0	0	11	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	15
	<i>Gymnotus coropinae</i>	0	2	1	0	1	0	0	0	0	0	0	1	16	13	2	0	0	0	3	1	7	4	51
	<i>Gymnotus curupira</i>	0	0	0	1	0	0	7	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9
Hypopomidae	<i>Brachyhypopomus batesi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	4	0	0	0	0	9
	<i>Brachyhypopomus beebei</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Brachyhypopomus cf. brevirostris</i>	1	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
	<i>Brachyhypopomus hamiltoni</i>	3	0	1	0	0	0	1	0	0	0	0	4	3	11	0	1	0	2	0	1	5	0	32
	<i>Hypopygus lepturus</i>	0	1	2	0	0	0	3	0	0	0	0	0	2	0	12	0	4	0	0	0	0	0	24
	<i>Microsternarchus bilineatus</i>	1	0	0	0	0	0	0	0	0	0	0	0	5	0	0	2	5	4	4	2	2	14	39
Cyprinodontiformes																								
Rivulidae	<i>Laimosemion kiroviskyi</i>	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	2	1	12
	<i>Anablepsoides micropus</i>	0	0	0	1	0	0	0	0	0	2	0	0	2	2	2	0	0	0	9	2	0	0	20
Beloniformes																								
Belonidae	<i>Belonion apodion</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Synbranchiformes																								
Synbranchidae	<i>Synbranchus madeirae</i>	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	5
	<i>Synbranchus sp.</i>	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	7
Cichliformes																								
Cichlidae	<i>Aequidens tetramerus</i>	1	11	0	3	3	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	21
	<i>Crenicichla inpa</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3
	<i>Apistogramma agassizii</i>	0	2	0	0	14	4	27	0	0	1	0	0	0	0	11	19	66	32	11	1	10	2	200

	Round 1											Round 2																
	CATCHM. 1			CATCHM. 2				CATCHM.3					CATCHM. 1			CATCHM. 2				CATCHM.3								
<i>Apistogramma pallidus</i>	0	0	0	0	0	0	0	55	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56
<i>Apistogramma pulchra</i>	0	0	0	6	0	0	0	0	0	0	0	0	0	26	11	0	0	0	0	0	0	0	0	0	0	0	0	43
Eleotridae <i>Microphilypnus ternetzi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	2	0	0	0	0	0	0	0	0	11	
Number of species	19	17	16	14	14	9	12	7	6	11	7	5	20	12	18	10	18	19	10	7	13	6					<u>270</u>	
Number of individuals	116	106	127	60	57	69	104	91	15	83	28	13	381	310	156	192	891	195	86	9	104	23					<u>3216</u>	

Table 2. Analysis of variance results (ANOVA) and the mean and range of environmental variables in the two sampling years in Purus-Madeira interfluve, Brazil. Bold values correspond to $P < 0.001$.

Abiotic variables	2015	2016	F	P-value
leaf %	0.67 [0.4 – 0.92]	0.63 [0.48 – 0.92]	0.4	0.5
fine leaf %	0.14 [0 – 0.33]	0.18 [0 – 0.63]	0.6	0.4
trunk %	0.07 [0 – 0.18]	0.09 [0 – 22]	0.1	0.7
roots %	0.003 [0 – 0.03]	0.01 [0 – 0.11]	0.8	0.3
clay %	0.09 [0 – 0.33]	0.07 [0 – 0.22]	0.3	0.5
pH	4.16 [3.58 – 4.49]	3.87 [3.37 – 4.7]	0.05	0.8
Temp. (°C)	25.9 [25.26 – 26.77]	24.87 [23.22 – 26.03]	17.8	0.0004
Conductivity ($\mu\text{S cm}^{-1}$)	17.25 [9 – 24]	14.27 [10 – 23]	1.18	0.2
Dissolved O ² (mg L ⁻¹)	14.7 [13.3 – 17.6]	17.56 [8.2 – 45.6]	0.9	0.3
Mean Depth (cm)	27.9 [13.6 – 56]	27.13 [10 – 68.23]	0.03	0.8
Mean width (cm)	218.94 [120.3 – 427]	235.37 [113.1 – 374]	0.18	0.6
Mean flow (m s ⁻¹)	0.051 [0 – 0.035]	0	17.94	0.0004

Table 3. Probability associated with each predictor variable in the linear mixed-effects models (LMM) for trajectory length values, species gain and species losses metrics as function of temperature and flow velocity difference and inundation connectivity values. Catchment was considered a random effect in all models. Marginal R² values are for the models adjusted only considering fixed effects. Bold values correspond to $p < 0.05$.

	Temperature difference	Flow velocity difference	Inundation mean value	R ² marginal
Trajectory length	0.82	0.29	0.01	0.56
Species gain	0.48	0.78	0.03	0.40
Species losses	0.25	0.83	0.2	0.27

FIGURAS

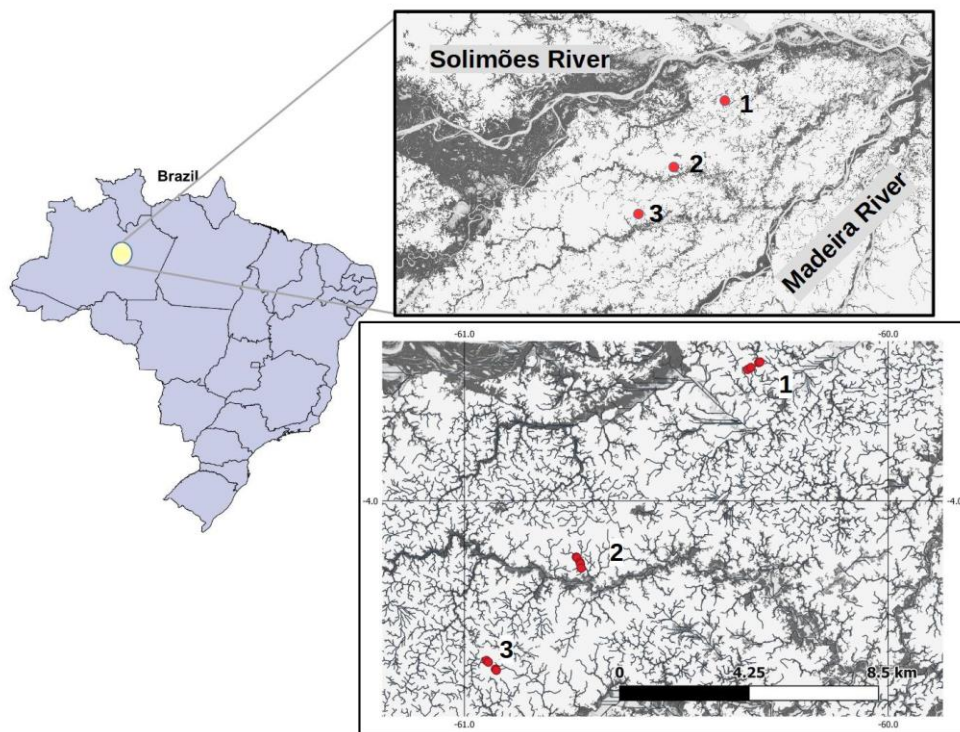


Figure 1. Map of the study area showing the three catchments and the 11 streams reaches analyzed in the Purus-Madeira interfluvium, Central Amazonia, Brazil.

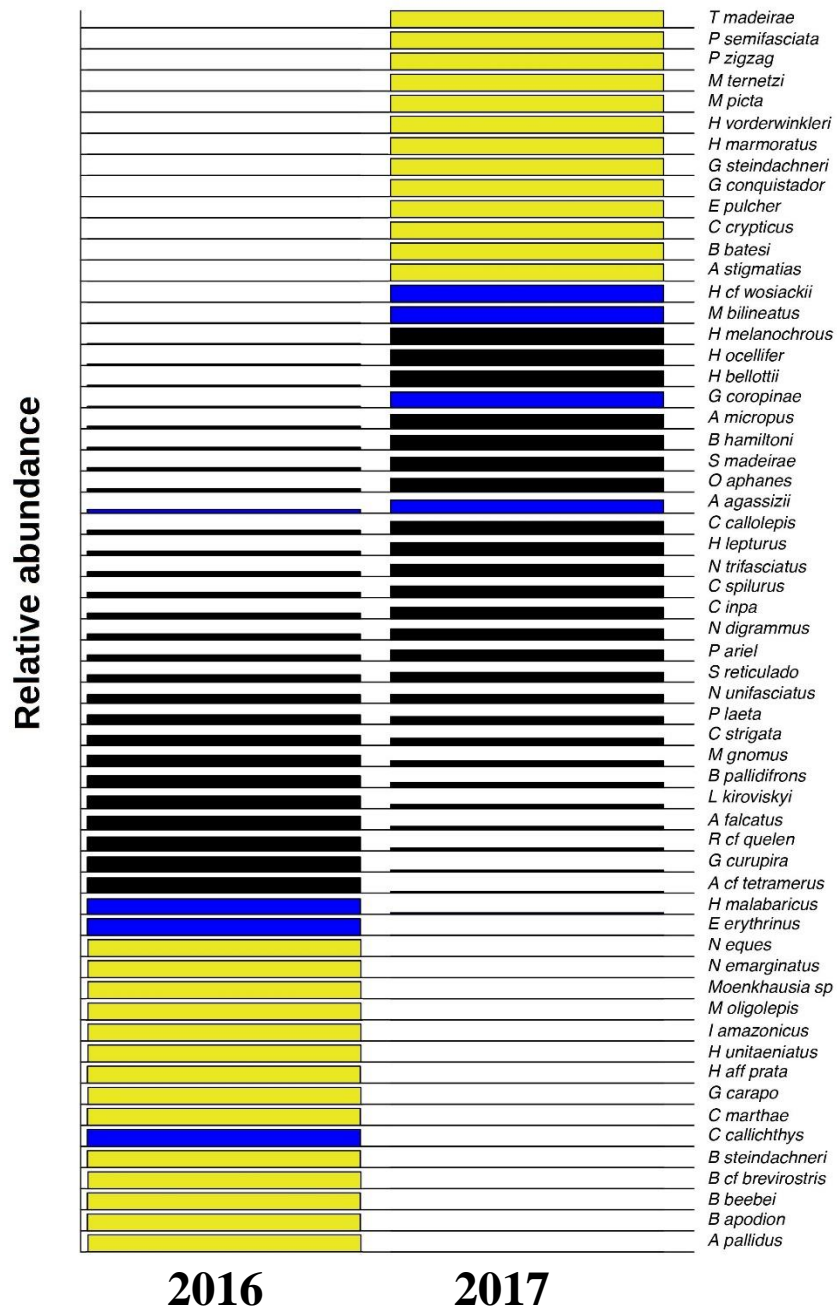


Figure 3. Relative abundance of stream fish species sampled between 2016 and 2017. Yellow bars indicate species collected only in one year and blue bars represent species indicate by INDVAL results as being significantly more abundant in one of the years.

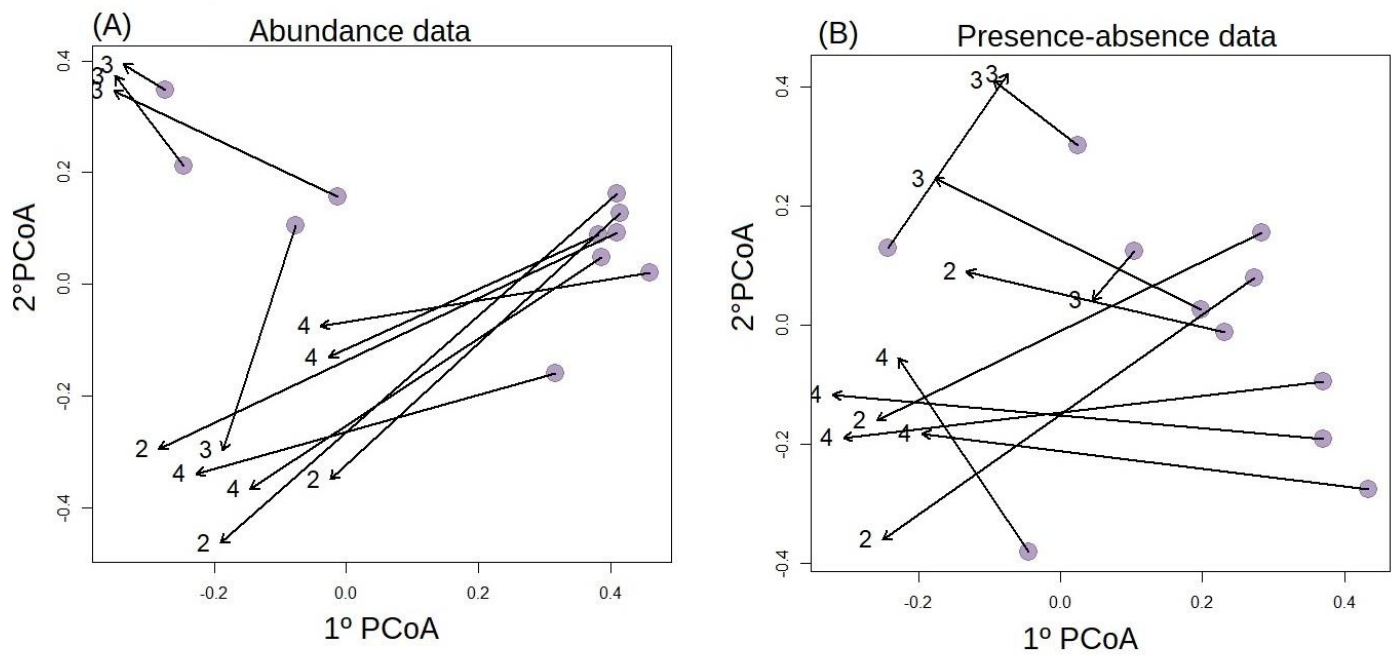


Figure 4. Principal coordinates analysis (PCoA) based on (A) species-abundance dissimilarities and (B) presence-absence data, showing the variation in fish assemblages from 2016 (purple circles) to 2017 (arrowhead). Numbers represents the catchments.

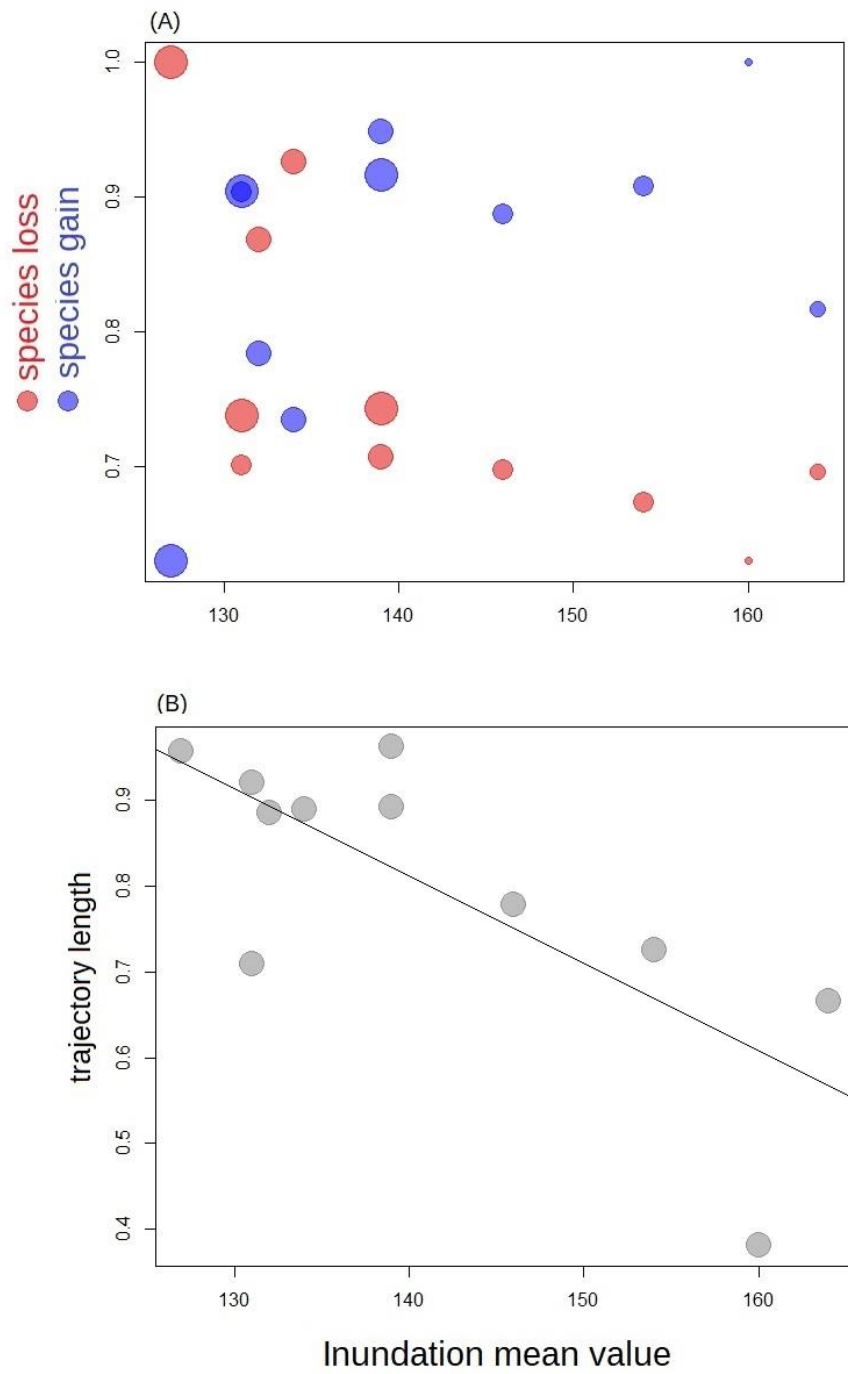


Figure 5. Relationship between (A) species gain and loss and (B) trajectory length of stream fish assemblages and floodplain connectivity.

SÍNTESE

Demonstramos nessa tese que o interflúvio Purus-Madeira possui uma rica fauna de peixes de riacho, cujos padrões de diversidade em escala temporal e espacial são principalmente estruturados pela conectividade com a planície de inundação das grandes drenagens.

No primeiro capítulo nós fornecemos uma lista atualizada da ictiofauna de riachos do interflúvio Purus-Madeira, elaborada a partir de um amplo esforço amostral tanto em escala espacial como temporal e também a partir dos registros de ocorrência realizados anteriormente. Nossa lista final, composta por 184 espécies, evidencia a rica fauna de peixes que habita essas drenagens e o quanto nosso conhecimento sobre a biodiversidade desses sistemas ainda carece de aprofundamento, uma vez que 34 espécies ainda apresentam status taxonômico indefinido. O alto número de espécies e de indivíduos encontrados é um indício que processos ecológicos que regulam a coexistência de espécies no espaço e no tempo nesses sistemas são diferentes daqueles já relatados para outros riachos da Amazônia central e que precisam ser melhor compreendidos. Essa lista é um importante subsídio para novos estudos na região e ajuda na delimitação de áreas que precisam ser melhor investigadas.

No segundo capítulo analisamos os padrões de dissimilaridade em amplas escalas geográficas e demonstramos que há uma diminuição no número de espécies nos riachos posicionados nas cabeceiras das drenagens, enquanto que as assembleias de drenagens curtas e próximas aos grandes rios são mais diversas. Nossos resultados também indicaram uma perda de diversidade funcional em direção as cabeceiras, onde as espécies tendem a ser menores e com maior capacidade de natação, enquanto que drenagens mais conectadas à planície de inundação abrigam mais espécies bentônicas e de maior porte. Nós não encontramos relação entre as condições locais e os padrões de diversidade, o que pode ser um indício de que nesses ambientes as assembleias são principalmente estruturadas por fatores regionais, que regulam a dispersão de indivíduos entre habitats. No entanto, é preciso ter em mente que a capacidade de detectar efeitos locais tende a diminuir quando ampliamos a escala analisada e que nós não descartamos a possibilidade das variáveis locais estarem atuando na segregação das espécies em

pequena escala. Os padrões de diversidade também não estiveram relacionados a distância por água, o que sugere que, apesar da distância geográfica representar uma barreira pra grande parte das espécies de peixes de riacho, os ciclos frequentes de cheia e seca que esses riachos estão submetidos determinam padrões de estruturação fortemente associada ao eixo longitudinal das drenagens, fazendo com que riachos distantes geograficamente mais posicionados de forma similar com relação a planície de inundação, abriguem grupos similares de espécies e de traços funcionais. Abordagens macroecológicas que incorporem informações de outras drenagens podem ajudar a melhor destrinchar os efeitos da formação geológica, de processos históricos e de variáveis climas nesses padrões.

No terceiro capítulo nós avaliamos a estabilidade interanual das assembleias de peixes de riachos intermitentes, que são bastante comuns nas drenagens do interflúvio Purus-Madeira. Nós encontramos uma variabilidade interanual significativa na composição das assembleias, devido a uma alta substituição de espécies raras e grandes oscilações de abundância entre anos. Esse padrão difere daquele encontrado em riachos perenes na Amazônia Central, onde as espécies são bastantes persistentes entre anos e as assembleias tendem a retornar para um estado inicial, após oscilações sazonais. A planície de inundação parece atuar como amortecedor dos efeitos estocásticos de extinção e colonização, uma vez que as assembleias mais conectadas a áreas alagáveis tiveram composição mais estável entre anos. Estudos com intervalos de tempos menores podem ajudar a compreender se a variabilidade que encontramos está relacionada a diferentes tempos de estabilização devido a diferentes tipos de conectividade com a planície de inundação ou se as espécies que chegam primeiro determinam diferentes processos de colonização e conseqüentemente diferentes estados intermediários ao longo do tempo. Monitoramentos de longo prazo também são fundamentais para aprofundar nosso conhecimento sobre a dinâmica hidrológica desses ambientes e quais as características geomorfológicas e climáticas que determinam a ocorrência de sistemas intermitentes na Amazônia. Essas informações podem ajudar a mapear outras áreas potenciais de ocorrência de drenagem com regimes intermitentes e melhorar nossas previsões sobre os impactos das mudanças climáticas sobre os sistemas aquáticos.

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