



Universidade Federal do Rio Grande
Instituto de Ciências Biológicas
Pós-graduação em Biologia de
Ambientes Aquáticos Continentais



Facetas da diversidade de peixes em riachos de terra firme na Amazônia: fatores estruturantes em múltiplas escalas

André Ribeiro Martins

Orientador: Dr. Luiz Ubiratan Hepp

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Aluno: André Ribeiro Martins

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ATA DE DEFESA DE TESE DE DOUTORADO EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS – Nº 001/2025

Às 09h00 (nove horas) do dia 18 (dezoito) do mês de fevereiro de 2025 (dois mil e vinte e cinco), via Webconferência no endereço eletrônico: (<http://meet.google.com/yyr-yrix-nay>) reuniram-se docentes, discentes e comunidade em geral, para a Defesa Pública da Tese de Doutorado do acadêmico André Ribeiro Martins. A Tese intitulada “**Facetas da diversidade de peixes em riachos de terra firme na Amazônia: fatores estruturantes em múltiplas escalas**” foi avaliada pela Banca Examinadora composta pelo Profº Dr. Luiz Ubiratan Hepp (Orientador); Profª Dra. Adriana Gava (FURG); Profº Dr. Anderson Ferreira (UFGD) e Profº Dr. André Luiz Machado Pessanha (UEPB). Após a defesa e arguição pública, a Banca Examinadora reuniu-se, para deliberação final, e considerou o acadêmico **APROVADO**. Desta forma, o acadêmico concluiu mais uma das etapas necessárias para a obtenção do grau de **DOUTOR EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS**. Nada mais havendo a tratar, às 12h00h (doze horas) foi lavrada a presente ata, que lida e aprovada, foi assinada pelos membros da Banca Examinadora, pelo Acadêmico e pelo Coordenador do Curso.

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DEDICATÓRIA

Dedico essa tese à minha mãe.

EPÍGRAFE

Quando a vida te decepçiona, qual é a solução?
Continue a nadar!
Dori, Procurando Nemo

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Escrever os agradecimentos desta Tese soa surreal. Espero, em algum momento, entender os caminhos que me conduziram até aqui, assim como entender e absorver que o normal é concluir esta etapa com mais dúvidas do que certezas. O conteúdo deste documento não foi construído apenas com os caminhos percorridos ao longo dos últimos quase 5 anos, mas também com aqueles que sequer existiram. Que o André do futuro encontre algumas respostas e continue com muitas dúvidas, e que nesse futuro essas respostas sejam encontradas com menos análises estatísticas. Agradeço aos meus queridos amigos, que confiaram em mim, mesmo sem conhecer os detalhes deste trabalho. Obrigado!"

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RESUMO

A literatura tem apontado que as comunidades biológicas são estruturadas por uma combinação de processos que ocorrem em múltiplas escalas, onde em amplas escalas espaciais e temporais, processos históricos de especiação, extinção e dispersão são responsáveis pela formação do conjunto regional de espécies. Por sua vez, em escalas menores de tempo e espaço, processos ecológicos contemporâneos (i.e., filtragem ambiental) são responsáveis pela determinação dos padrões de composição e diversidade nas comunidades locais. A presente Tese investiga os fatores que influenciam a composição e diversidade de peixes de riachos amazônicos, adotando uma abordagem multifacetada que integra as facetas taxonômica, funcional e filogenética da biodiversidade. Para isso, utilizamos um extenso banco de dados de peixes e de características ambientais locais de 30 pequenos riachos de terra firme (i.e., não inundáveis) da Volta Grande do Xingu, inventariados entre os anos de 2012 e 2023. Observamos que a limitação de dispersão, as condições ambientais em múltiplas escalas e a conectividade explica boa parte estrutura das assembleias de peixes desses sistemas, enquanto interações interespecíficas (por exemplo, competição), parecem ter pouca influência na dinâmica e distribuição das espécies de peixes nas assembleias. Observamos que tanto a diversidade funcional quanto a diversidade filogenética são explicadas pelas condições ambientais e pela conectividade. Além disso, a singularidade funcional, que destaca a presença de características únicas nas assembleias locais, está fortemente associada às condições ambientais. Por outro lado, a singularidade filogenética, que mede o quanto as espécies de um determinado local são únicas em termos de sua história evolutiva em comparação com outros locais, é explicada por uma combinação de fatores ambientais e conectividade. Exploramos a dinâmica temporal das assembleias de peixes, focando no impacto de eventos de secas extremas na diversidade beta temporal, que mede a variação na composição de espécies ao longo do tempo. Tanto em riachos perenes quanto naqueles afetados pela perda do fluxo, o componente de substituição de espécies foi o principal responsável pela diversidade beta temporal, indicando que a mudança na composição das comunidades de peixes ao longo do tempo é devido à entrada e saída de espécies, e não à formação de subconjuntos aninhados de espécies. Embora a substituição seja o componente dominante em ambos os tipos de riachos, os eventos de secas extremas amplificam esse mecanismo. As informações presentes nesta Tese demonstram a necessidade de avaliar múltiplas facetas da biodiversidade (taxonômica, funcional e filogenéticas) e destacam a necessidade do monitoramento ecológico contínuo e de longo prazo dos sistemas naturais.

Palavras-chave: metacomunidades, peixes de riachos, ictiofauna amazônica, singularidade ecológica

ABSTRACT

Recent literature has indicated that biological communities are structured by a combination of processes that occur at multiple scales. At broad spatial and temporal scales, historical processes of speciation, extinction, and dispersal are responsible for the formation of the regional species pool. In turn, at smaller temporal and spatial scales, contemporary ecological processes (i.e., environmental filtering) are responsible for determining the patterns of composition and diversity in local communities. This Thesis investigates the factors that influence the composition and diversity of fish in Amazonian streams, adopting a multifaceted approach that integrates the taxonomic, functional, and phylogenetic facets of biodiversity. To this end, we used an extensive database of fish and local environmental characteristics from 30 small terra firme streams (i.e., non-floodable) in the Volta Grande do Xingu, surveyed between 2012 and 2023. We observed that dispersal limitation, environmental conditions at multiple scales, and connectivity explain much of the structure of fish assemblages in these systems, while interspecific interactions (e.g., competition) seem to have little influence on the dynamics and distribution of fish species in the assemblages. We observed that both functional diversity and phylogenetic diversity are explained by environmental conditions and connectivity. Furthermore, functional singularity, which highlights the presence of unique characteristics in local assemblages, is strongly associated with environmental conditions. On the other hand, phylogenetic singularity, which measures how unique the species of a given location are in terms of their evolutionary history compared to other locations, is explained by a combination of environmental factors and connectivity. We explored the temporal dynamics of fish assemblages, focusing on the impact of extreme drought events on temporal beta diversity, which measures the variation in species composition over time. In both perennial streams and those affected by flow loss, the species replacement component was the main driver of temporal beta diversity, indicating that the change in the composition of fish communities over time is due to the entry and exit of species, and not to the formation of nested subsets of species. Although replacement is the dominant component in both types of streams, extreme drought events amplify this mechanism. The information presented in this Thesis demonstrates the need to assess multiple facets of biodiversity (taxonomic, functional, and phylogenetic) and highlights the need for continuous long-term ecological monitoring of natural systems.

Key-words: metacommunities, stream fish, amazonian ichthyofauna, ecological uniqueness

APRESENTAÇÃO

Esta Tese segue o modelo de formatação sugerido pelo Programa de Pós-graduação em Biologia de Ambientes Aquáticos Continentais (PPGBAC) da Universidade Federal do Rio Grande (FURG). A Introdução Geral contém o arcabouço teórico do tema em estudo, bem como os objetivos que serão investigados nos capítulos; esta seção está formatada seguindo as normas da Associação Brasileira de Normas Técnicas (ABNT). O primeiro capítulo da tese intitulado “*Metacommunity organisation of Amazonian stream fish assemblages: The importance of spatial and environmental factors*” segue as normas de formatação e está publicado no periódico Ecology of Freshwater Fish (Qualis Capes: A2, IF: 1.6). Neste capítulo, utilizamos modelagem hierárquica conjunta de distribuição de espécies para verificar a efeitos de fatores ambientais (em múltiplas escalas espaciais), da configuração da rede de drenagem, da autocorrelação espacial e interações interespecíficas na estrutura de assembleias de peixes em riachos de terra firme da Amazônia. O segundo capítulo, “*The role of the environment and connectivity on multiple facets of local fish diversity in tropical headwater streams*” segue as normas de formatação e está publicado no periódico Freshwater Biology (Qualis Capes: A1, IF: 2.8). Neste capítulo avaliamos as contribuições das condições ambientais, da conectividade dos corpos d'água na rede de drenagem e dos fatores espaciais para a estrutura funcional e filogenética da ictiofauna desses pequenos riachos. No terceiro capítulo, intitulado “*Drought intensification drives variation in temporal species turnover in Amazonian stream fish assemblages*” avaliamos como as mudanças temporais na composição de espécies promovidas pela perda de fluxo afetam os componentes da diversidade beta temporal. O terceiro capítulo está sendo preparado e segue as normas do periódico Freshwater Biology (Qualis Capes: A1, IF: 2.8). Finalizamos com a seção de Considerações Finais e Perspectivas obtidas com o desenvolvimento da Tese; nesta última seção, as citações e referências bibliográficas seguem as normas da ABNT.

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Table S1 Summary of fish collection activities and environmental variables in each stream during the 12 sampling campaigns conducted between March 2012 and October 2014 in the region of Volta Grande do Xingu, Pará state, Brazilian Eastern Amazon. 1 = Sampling successfully performed; 2 = Streams that dried up or with no flow (isolated ponds); 3 = Very high-water volume (no conditions to perform standardized sampling); 4 = No access to the site (trail closed by vegetation or blocked road); 5 = Collection point had not yet been implemented; 6 = Collection point is no longer inventoried. * = Sampling selected in the rainy season; # = sampling selected during the dry season.

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Capítulo 3

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2023, in the region of Volta Grande do Xingu, Pará state, Brazilian Eastern Amazon. 1 = Sampling successfully performed; 2 = Streams that dried up or with no flow (isolated ponds); 3 = Very high-water volume (no conditions to perform standardized sampling); 4 = No access to the site (trail closed by vegetation or blocked road); 5 = Collection point had not yet been implemented; 6 = Collection point is no longer inventoried.* = sampling was carried out, however, no specimen was collected.

Table S2 List of fish species sampled in 23 streams in the region of Volta Grande do Xingu, state of Pará, Brazilian Eastern Amazon. Occurrence refers to the total number of streams where the species were found.

Table S3 Results from the model selection for general linear models (according to the Akaike information criterion) evaluating the effect of the hydrological state and its interactions with time between sampling events, slope catchment, stream link magnitude (Link), downstream link (D-link), extension of the drainage network (EDN), and distance from the mainstream (DMS), and the environmental variability (EV) as explanatory variables on temporal β -diversity and its components, turnover and nestedness, and for on standard effect size (SES) values of temporal β -diversity and its components, turnover and nestedness. Models excluding outliers.

Table S4 One-sample t-test and Wilcoxon rank-sum test were used to assess whether SES indices differed from zero in each hydrological state. The test statistic (t or W), degrees of freedom (for t-tests only), and p-values are reported.

INTRODUÇÃO GERAL

Identificar os processos responsáveis pela distribuição dos organismos no espaço e no tempo é uma tarefa complexa e estimulou o desenvolvimento de muitas teorias, conceitos e hipóteses ao longo do tempo (VELLEND, 2010, 2016), devido a influência de inúmeros processos que ocorrem em múltiplas escalas, tanto espaciais quanto temporais (ALLAN; CASTILLO, 2007; HOEINGHAUS; WINEMILLER; BIRNBAUM, 2007; VELLEND, 2016). Considerar que processos ocorrendo em diferentes escalas são responsáveis por modular a composição e diversidade de comunidades locais gerou avanços consistentes na ecologia de comunidades (WINEGARDNER *et al.*, 2012). Entre esses avanços, a teoria de metacomunidade tem sido amplamente utilizada para explicar os padrões de distribuição de muitos grupos, como peixes (PALHETA *et al.*, 2021), morcegos (BOGONI; CARVALHO-ROCHA; DA SILVA, 2022; PRESLEY; WILLIG, 2022), invertebrados (CUNHA; JÜEN, 2020; TONKIN *et al.*, 2015) e plantas (GONZÁLEZ-CARO *et al.*, 2021; OLIVEIRA *et al.*, 2018).

Em sua síntese inicial, LEIBOLD *et al.* (2004) definiram uma metacomunidade como um “conjunto de comunidades locais conectadas pela dispersão de múltiplas espécies potencialmente interativas (GILPIN; HANSKI, 1991; WILSON, 1992)”, e partir desses pressupostos, quatro mecanismos (arquétipos) foram propostos para agrupar os processos responsáveis pelos padrões de distribuição das espécies nas comunidades biológicas: **alocação de espécies** (*species sorting*), **efeito de massa** (*mass effect*) (Shmida & Wilson 1985), **dinâmica de manchas** (*patch dynamics*) (Levins & Culver 1971) e **neutro** (*neutral*) (HUBBELL, 2001). Esses mecanismos são estruturados com base em duas questões centrais: se existe e qual a capacidade de dispersão das espécies que integram as comunidades; e se as espécies respondem e como elas respondem às mudanças nas condições ambientais (WINEGARDNER *et al.*, 2012). Com isso, em ambientes altamente heterogêneos, diferenças entre as comunidades seriam causadas por filtros ambientais e/ou interações entre as espécies, resultando em uma metacomunidade estruturada por **alocação de espécies** (LEIBOLD *et al.*, 2004). O **efeito de massa** ressalta a dispersão de indivíduos como fator chave na dinâmica de organização local, onde a troca de indivíduos pode resgatar populações que tenham desaparecido de um determinado local ou ainda permitir que algumas populações se mantenham em locais desfavoráveis (LEIBOLD *et al.*, 2004). No mecanismo da **dinâmica de manchas**, o ambiente é visto como manchas de habitat similares, capazes de conter populações de diferentes espécies; nesse mecanismo, os filtros ambientais não atuam, com

isso, a dispersão e a interação entre as espécies tornam-se um fator chave no padrão de distribuição das espécies nas comunidades (LEIBOLD *et al.*, 2004). O **modelo neutro** assume que todas as espécies são semelhantes em suas capacidades competitivas, onde a organização das espécies nas comunidades é o resultado da movimentação aleatória das espécies (LEIBOLD *et al.*, 2004).

A distinção dos mecanismos responsáveis por estruturar as comunidades biológicas em arquétipos (categorias) discretos ignoram a existência de numerosos processos implícitos a esses mecanismos, como, por exemplo, interações entre espécies, que embora sejam reconhecidas nos modelos clássicos não levam em consideração a capacidade competitiva (LEIBOLD *et al.*, 2022; THOMPSON *et al.*, 2020). Isso ocorre porque a estrutura de metacomunidade proposta por LEIBOLD *et al.* (2004) considera que os processos operam de forma semelhante em todas as espécies e comunidades (locais), o que pode levar a uma interpretação de que a metacomunidade analisada poder ser estruturada por um único mecanismo, ignorando totalmente como cada espécie e local contribui para estruturação das comunidades (LEIBOLD *et al.*, 2022). Mesmo estudos que buscaram subdividir as comunidades e analisar os mecanismos em grupos, como por exemplo, espécies satélites e centrais (VIEIRA *et al.*, 2020) ou espécies com alta e baixa capacidade de dispersão (PALHETA *et al.*, 2021), esses processos sutis ainda são negligenciados. Reconhecer que um contínuo de processos bióticos e abióticos dão origem aos padrões de composição e diversidade das comunidades biológicas (BROWN *et al.*, 2017) levou a reestruturação da teoria de metacomunidades (LEIBOLD *et al.*, 2022; THOMPSON *et al.*, 2020). THOMPSON *et al.*, 2020 buscaram expandir a teoria para além dos arquétipos, enfatizando a importância de considerar a variação contínua dos processos subjacentes. Por sua vez, LEIBOLD *et al.*, 2022, reconhecem a necessidade de analisar a heterogeneidade dentro das metacomunidades, focando nas contribuições específicas das espécies e dos locais para os padrões gerais.

A proposta de reestruturação da teoria de metacomunidades de THOMPSON *et al.* (2020) busca integrar teorias sobre coexistência em escala local (por exemplo, CHESSON, 2000; GAUSE, 1932; LOTKA, 1922; SHOEMAKER; MELBOURNE, 2016; VOLTERRA, 1926), que até agora foram negligenciadas em estudos de metacomunidades, com processos relacionados à heterogeneidade ambiental e dispersão (THOMPSON *et al.*, 2020). Com isso, a dinâmica populacional e comunitária é governada pela interação de três processos fundamentais: (I) respostas independentes da densidade a condições abióticas, (II) interações bióticas dependentes da densidade e (III) dispersão; com a estocasticidade sendo incorporada em todos os três processos (THOMPSON *et al.*, 2020). O arcabouço teórico proposto por

THOMPSON et al. (2020) integra os arquétipos tradicionais (ou seja, ***alocação de espécies***, ***efeito de massa***, ***dinâmica de manchas*** e ***neutro***) da teoria de metacomunidades dentro de um processo contínuo definido pela variação na força dos três processos fundamentais, onde a localização precisa de cada arquétipo em um espaço tridimensional é determinada pela combinação específica desses processos. Com essa reestruturação, o arquétipo de ***alocação de espécies*** surge quando as respostas independentes da densidade à heterogeneidade abiótica são fortes e variam entre as espécies; a dispersão é considerada intermediária, permitindo que as espécies alcancem habitats favoráveis, mas não alta o suficiente para homogeneizar a metacomunidade. A ocorrência do ***efeito de massa*** compartilha as premissas da seleção de espécies, mas com taxas de dispersão mais altas, onde consequentemente, populações podem persistir em habitat desfavoráveis devido à constante entrada de indivíduos provenientes de locais mais adequados. A ***dinâmica de manchas*** surge quando a competição interespecífica desempenha um papel fundamental, onde espécies competem por recursos, e a coexistência regional depende de um trade-off entre capacidade competitiva e colonização. Espécies dominantes, com menor dispersão, são superiores na competição, enquanto espécies com menor capacidade competitiva se dispersam com maior facilidade, colonizando novas manchas. Além disso, o surgimento do arquétipo da dinâmica de manchas considera a existência de extirpações locais. O ***modelo neutro*** ocorre quando as espécies apresentam respostas idênticas à heterogeneidade ambiental e competem igualmente pelos recursos e a capacidade de dispersão é limitada.

A composição e diversidade das comunidades biológicas depende da configuração espacial do ecossistema e do grupo estudado, devido a capacidade dispersão e processos baseados em nicho (HEINO, 2013; HEINO *et al.*, 2015a; SCHMERA *et al.*, 2018; TONKIN *et al.*, 2018). Para organismos estritamente aquáticos como os peixes, a conectividade (configuração espacial) dos sistemas fluviais é um fator chave na dinâmica de distribuição das espécies, por limitar a ocorrência nos tributários (ramos) e canais principais (troncos principais) (HEINO *et al.*, 2015a, 2015b). Essa configuração é ainda mais importante para ictiofauna de pequenos riachos de cabeceiras que é composta principalmente por espécies de pequeno porte não migratórias (CASTRO, 1999; MENDONÇA; MAGNUSSON; ZUANON, 2005). Com isso, a característica dendrítica da rede de drenagem limita a dinâmica de dispersão e colonização local, pois as variáveis estruturais (físicas e químicas) existentes nos pequenos riachos são distintas daquelas observadas em corpos hídricos maiores (BROWN *et al.*, 2011). Essas diferenças fazem com que algumas espécies não consigam se deslocar entre riachos de pequena ordem, quando eles estão conectados por sistemas muito maiores

(BROWN *et al.*, 2011; FAGAN, 2002). Assim, espera-se que a similaridade da ictiofauna diminua com a distância (geográfica ou fluvial) devido ao efeito do isolamento causado por barreiras físicas e mudanças no gradiente ambiental (FAGAN, 2002). Além disso, a posição do riacho com relação aos grandes rios pode potencializar o recrutamento das populações que habitam essa interface, onde riachos com características estruturais semelhantes tendem a apresentar assembleias de peixes distintas de acordo com a sua posição dentro da rede de drenagem (LAMPERT *et al.*, 2018; STEGMANN *et al.*, 2019).

A Bacia Amazônica abriga ~ 15 % (2.716 espécies validas) de todas as espécies de peixes de água doce do mundo (DAGOSTA; PINNA, 2019; TEDESCO *et al.*, 2017). Entre as várias hipóteses que buscam explicar a origem e a manutenção dessa biodiversidade, as baixas taxas de extinção de espécies ao longo do tempo, devido à alta diversidade de habitat aquáticos e a maior estabilidade climática desde o último período glacial tem sido considerados os fatores mais importantes (HOORN *et al.*, 2010; JUNK; SOARES; BAYLEY, 2007; OBERDORFF *et al.*, 2019). Essa alta diversidade de habitat é bem conhecida pelos grandes rios e por suas vastas planícies de inundação (CRAMPTON, 2011). No entanto, um complexo sistema de pequenos riachos que drenam florestas de terra firme localizados fora do alcance do pulso de inundação unimodal regular e previsível que sofrem os grandes rios e planícies, contribui para a formação dos afluentes dos rios amazônicos (JUNK; BAYLEY; SPARKS, 1989; JUNK; SOARES; BAYLEY, 2007). Esses riachos de terra firme ou de cabeceiras são sistemas oligotróficos (ANJOS, 2013; CASTRO, 1999; VANNOTE *et al.*, 1980) influenciados por chuvas em suas áreas de drenagem, respondendo rapidamente à precipitação local (ESPÍRITO-SANTO *et al.*, 2009).

A ictiofauna que ocorre em riachos apresenta uma estreita relação com as condições ambientais, onde as características desses ambientes, como, largura, velocidade da água, profundidade e cobertura do dossel são fatores primários na determinação da riqueza e composição das assembleias locais (ANGERMEIER; KARR, 1983; FERNANDES *et al.*, 2013; HARDING; BURKY; WAY, 1998; LEITÃO *et al.*, 2018; MENDONÇA; MAGNUSSON; ZUANON, 2005). No entanto, essas variáveis em escala local são influenciadas por variáveis na escala de drenagem, como, por exemplo, geologia, clima e estrutura da vegetação da bacia hidrográfica (BENONE *et al.*, 2017; FRISSELL *et al.*, 1986). Assim, a influência das condições ambientais nos padrões de composição e diversidade das assembleias de peixes opera em diferentes escalas espaciais (HOEINGHAUS; WINEMILLER; BIRNBAUM, 2007; MACEDO *et al.*, 2014; PALLER *et al.*, 2016).

Além das condições ambientais e de fatores espaciais, filtros bióticos são apontados como um dos condutores dos padrões de composição e diversidade das comunidades locais (VELLEND, 2016). Nesse sentido, os processos de interação biótica parecem ser mais evidentes em comunidades menos diversas (SAAVEDRA *et al.*, 2017). Até o momento não está claro como as interações bióticas influenciam na organização de comunidades ricas em espécies e com alta heterogeneidade ambiental, como por exemplo a ictiofauna de riachos amazônicos. As novas propostas de dinâmica de metacomunidades (i.e., LEIBOLD *et al.*, 2021; THOMPSON *et al.*, 2020) incorporam as terias de coexistência local para estabelecer que as interações interespecíficas são fundamentais nos processos de estruturação das metacomunidades. De maneira ampla, as teorias de coexistência local reconhecem que os processos de interações interespecíficas ocorrem quando os organismos afetam a disponibilidade de recursos comuns a diferentes espécies, como por exemplo, espaço e disponibilidade de nutrientes (ADLER *et al.*, 2018; CHESSON, 2000; SHOEMAKER; MELBOURNE, 2016).

Por muito tempo, estudos em Ecologia de Comunidades concentraram seus esforços na abordagem taxonômica da biodiversidade, o que torna limitada a interpretação como os processos evolutivos e ecológicos contribuem para estruturação das comunidades biológicas (GIRARDELLO *et al.*, 2019; MOUILLOT *et al.*, 2013). Nesse sentido, a diversidade funcional tem ganhado espaço em estudos de ecologia de comunidades de peixes em riachos (TERESA; RODRIGUES-FILHO; LEITÃO, 2021). A abordagem funcional baseia-se em características (atributos funcionais) que podem ser medidas em qualquer nível relevante de organização biológica, como características morfológicas ou fisiológicas. Essas características estão relacionadas com o desempenho dos organismos e com a forma como respondem ou influenciam o funcionamento dos ecossistemas (DÍAZ; CABIDO, 2001; VIOLLE *et al.*, 2007). Por isso, a diversidade funcional pode ser mais sensível aos filtros ambientais do que a diversidade taxonômica, pois reflete a adaptação das espécies às condições locais (DÍAZ; CABIDO, 2001; VILLÉGER *et al.*, 2010). Além da diversidade funcional, a diversidade filogenética, que considera a história evolutiva dos organismos nas comunidades (JONES; BARBER; GIBSON, 2019), pode fornecer informações de como a interação entre a história evolutiva e os processos ecológico, como filtragem ambiental e competição, contribuem para a montagem da comunidade em escalas locais e regionais (BARBER *et al.*, 2017; GERHOLD *et al.*, 2015; JONES; BARBER; GIBSON, 2019). Assim, a diversidade filogenética pode ser usada para testar hipóteses sobre como a história evolutiva de uma comunidade influencia sua resposta, por exemplo, a distúrbios ambientais, espécies

invasoras e mudanças no gradiente ambiental, revelando padrões que não seriam aparentes apenas com medidas de diversidade taxonômica ou funcional. Essas facetas (funcional e filogenética) da biodiversidade merecem atenção nos estudos ecológicos, pois, em escalas amplas, a formação do conjunto regional de espécies, atribuída a processos históricos e biogeográficos (por exemplo, especiação, extinção e dispersão) (VELLEND, 2016) marcam profundamente a estrutura filogenética e funcional das espécies presentes em uma região (CASTILLO-ESCRIVÀ *et al.*, 2017; MOHAMMED; BLASIUS; RYABOV, 2022; RODRIGUES-FILHO *et al.*, 2018; VILLALOBOS; RANGEL; DINIZ-FILHO, 2013).

A investigação da dinâmica temporal das comunidades sempre foi um dos temas centrais em estudo ecológicos. No entanto, até para os peixes, um dos grupos de organismos mais intensamente estudados, a avaliação da dinâmica temporal é incipiente quando comparada com estudos em escala espacial. Por exemplo, DIAS *et al.* (2016), analisaram 124 estudos sobre assembleias de peixes de riacho no Brasil, publicados entre 1987 e 2012, do total, apenas 9% dos estudos analisaram aspectos da variação temporal das assembleias. Além disso, 86% dos estudos analisaram um ano ou menos de eventos amostragens. Outra síntese recente analisou 307 artigos científicos com foco em algum aspecto da dinâmica temporal de peixes de água doce, nos quais 74% dos estudos se concentraram na América do Norte (52,1%) e Europa (22,1%), com apenas 9,85% de estudos realizados na América do Sul (CZEGLÉDI; SPECZIÁR; ERŐS, 2022). Esse menor volume de estudos investigando a dinâmica temporal da ictiofauna é preocupante devido às mudanças climáticas em curso no nosso planeta. Para prever como as comunidades biológicas respondem a essas mudanças, precisamos inicialmente reconhecer as dinâmicas temporais naturais das comunidades e suas idiosincrasias, para depois desembaraçar dos efeitos decorrentes de eventos extremos (DONOHUE *et al.*, 2016).

Secas e inundações são consideradas as principais formas de distúrbio natural em ecossistemas lóticos (LAKE, 2003, 2011). Contudo, esses eventos tornam-se mais preocupantes diante das mudanças climáticas em curso no nosso planeta, que preveem o aumento da frequência e da intensidade desses eventos climáticos, com regiões do globo onde antes não havia esses distúrbios passando a conviver com eles (IPCC, 2023; PRUDHOMME *et al.*, 2014). Atualmente, mais da metade da rede hidrológica global é constituída por trechos intermitentes (que deixam de fluir em algum momento ao longo do ciclo sazonal), com a grande maioria desses sistemas em regiões áridas e com valores irregulares de precipitação ao longo do ano (DATRY; LARNED; TOCKNER, 2014). Além disso, o aumento da frequência de eventos extremos de seca levará à mudança de numerosos riachos perenes para

intermitentes, onde sistemas que historicamente experimentaram uma maior estabilidade na disponibilidade do fluxo, passarão a sofrer com a perda de habitat para organismos aquáticos de maneira periódica (DÖLL; SCHMIED, 2012).

A interrupção do fluxo em sistemas perenes pode causar mudanças significativas, incluindo a extinção local de organismos não adaptados à secagem do canal (DATRY; LARNED; TOCKNER, 2014; MATTHEWS; MARSH-MATTHEWS, 2003). Estudos sobre as respostas da ictiofauna de riachos a secas extremas estão concentrados em sistemas intermitentes que experienciam secagens sazonais regulares dos canais, resultando em alta resistência e resiliência devido às adaptações a essas condições ambientais rigorosas (CZEGLÉDI; SPECZIÁR; ERŐS, 2022; LAKE, 2011; MATTHEWS *et al.*, 2013; MATTHEWS; MARSH-MATTHEWS, 2003). Na bacia do rio Xingu, Amazônia Oriental, pesquisas iniciais indicam que secas extremas, com interrupção do fluxo, leva a mudanças na composição de espécies de peixes em riachos de terra firme, com efeitos que podem durar a médio prazo (MARTINS *et al.*, 2022). Apesar da recuperação na estrutura geral das comunidades de peixes oito meses após os eventos de perda de fluxo, algumas espécies não retornaram aos níveis de abundância anteriores. Dentre as dezessete espécies que apresentaram declínio na abundância, sete não se recuperaram completamente, mesmo após dois anos (MARTINS *et al.*, 2022).

As comunidades biológicas estão em constantes mudanças ao longo do tempo (COLLINS, 2000; MAGURRAN *et al.*, 2010). Determinar o quanto dessas mudanças se deve a flutuações naturais e o quanto é resultado de eventos extremos é crucial para entender como esses eventos afetam nos padrões de organização das comunidades, especialmente em um cenário de eventos extremos cada vez mais frequentes. Nesse sentido, a diversidade beta temporal, que mede a variação na composição de espécies ao longo do tempo, pode ser uma ferramenta valiosa (DORNELAS *et al.*, 2013; LEGENDRE, 2019).

A diversidade beta temporal possui dois componentes principais: a substituição temporal de espécies, que reflete a renovação da comunidade com o desaparecimento e surgimento de espécies, e o aninhamento temporal, que ocorre quando amostras com menos espécies são subconjuntos de amostras mais ricas (BASELGA, 2010). A substituição temporal de espécies pode ser moldada por processos em diferentes escalas de tempo, desde taxas de especiação e extinção em escalas evolutivas até respostas das espécies a fatores como conectividade do habitat e eventos sazonais em escalas de tempo mais curtas (BOGOTÁ-GREGORY *et al.*, 2023; DOBROVOLSKI *et al.*, 2012; SAITO *et al.*, 2021; TONKIN *et al.*, 2017). No entanto, o papel do aninhamento temporal na diversidade beta temporal ainda não

é totalmente compreendido, mas estudos com assembleias de peixes amazônicos sugerem que seus valores são baixos tanto em grandes sistemas fluviais (ambientes altamente conectados e dinâmicos) quanto em pequenos riachos de terra-firme (BOGOTÁ-GREGORY *et al.*, 2023).

Objetivos

Objetivos gerais

O objetivo geral dessa Tese é investigar a influência de interações interespecíficas, da conectividade dos corpos hídricos na rede de drenagem, de variáveis ambientais, espaciais, temporais, incluindo eventos de secas extremas, na estrutura e diversidade de múltiplas facetas (taxonômica, funcional e filogenética) de assembleias de peixes de riachos de terra firme da Amazônia.

Objetivos específicos

- No primeiro capítulo, examinamos os efeitos das condições ambientais tanto locais quanto na escala da bacia, da estrutura da rede de drenagem, da autocorrelação espacial e de interações interespecíficas na dinâmica da metacomunidade de peixes em riachos de terra firme na Amazônia.
- No segundo capítulo, avaliamos as contribuições das condições ambientais, da conectividade dos corpos d'água na rede de drenagem e dos fatores espaciais para a estrutura funcional e filogenética da ictiofauna de riachos de terra firme na Amazônia.
- No terceiro capítulo, investigamos os efeitos de eventos de secas extremas na variação temporal dos padrões de substituição e aninhamento de metacomunidades de peixes em pequenos riachos de terra firme na Amazônia.

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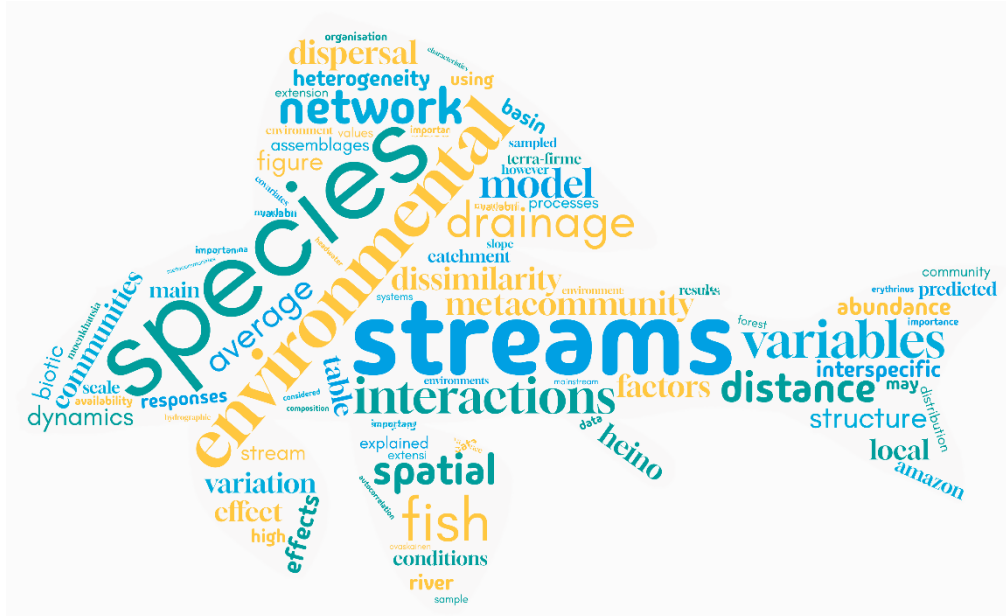
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Capítulo 1



Metacommunity organisation of Amazonian stream fish assemblages: The importance of spatial and environmental factors

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Abstract

Metacommunity theory seeks to explain how local and regional processes contribute to the organisation of biological communities. Recent conceptual frameworks of this theory indicate that the dynamics of populations and communities are jointly established by dispersal, species responses to environmental conditions and biotic interactions dependent on species density. Here, we use hierarchical joint species distribution modelling to verify the effects of environmental factors (at multiple spatial scales), drainage network configuration, spatial autocorrelation and interspecific interactions on the structure of fish assemblages in terra-firme streams in the Eastern Brazilian Amazon. Thirty streams were sampled in two field surveys, and 89 species were collected in total. Our results confirm the effects of limited dispersal, environmental conditions (at multiple scales) and the configuration of the drainage network on the dynamics of these assemblages. Furthermore, our results suggest that interspecific interactions are less relevant for the structuring of fish metacommunities in small Amazonian headwater streams. Abiotic factors like drainage networks and environmental heterogeneity were better predictors of species distributions than co-occurrence patterns with potential competitors or predators.

Keywords: community ecology, freshwater fish, ichthyofauna, interspecific interactions, metacommunity, riverine network

Introduction

Metacommunity theory has been widely used to explain the distribution patterns of many groups, such as fishes (Palheta et al., 2021; Vieira et al., 2020), bats (Bogoni et al., 2022; Presley & Willig, 2010), invertebrates (Cunha & Juen, 2020; Tonkin et al., 2015) and plants (González-Caro et al., 2021; Oliveira et al., 2018). Despite the important contributions of this theory to understanding the organisation of biological communities, most metacommunity studies are focused on discrete archetypes which ignore the existence of numerous processes implicit to them (e.g., niche breadth and species interactions) (Thompson et al., 2020). This focus imposes a limitation on the interpretation of continuous processes that take part in community organisation (Brown et al., 2017; Leibold et al., 2021; Thompson et al., 2020).

Recently, Thompson et al. (2020) reorganised the concept of metacommunities, proposing that population and community dynamics are governed by the interaction of three fundamental processes: (I) *density-independent responses to abiotic conditions*, (II) *density-dependent biotic interactions* and (III) *dispersal*, with stochasticity being incorporated in all three. Through these processes, Thompson et al. (2020) seek to unite theories regarding coexistence at the local scale (e.g. Chesson, 2000; Gause, 1932; Lotka, 1922; Shoemaker & Melbourne, 2016; Volterra, 1926), which until now have been neglected in metacommunity studies, with processes linked to environmental heterogeneity and dispersal (Thompson et al., 2020).

Metacommunity dynamics vary according to the spatial configuration of the ecosystem and the taxonomic groups present in the region, due to the effects of dispersal and niche-based processes (Heino, 2013; Heino, Melo, et al., 2015; Heino, Nokela, et al., 2015; Schmera et al., 2018; Tonkin et al., 2018). In river systems (Brown & Swan, 2010), the dispersal of strictly aquatic organisms (i.e. fish) is limited by tributaries (branches) and main channels (mainstems) (Heino, Melo, et al., 2015; Heino, Nokela, et al., 2015), and the position of these sites is key in the metacommunity dynamics of these systems (Lampert et al., 2018). Headwater streams are, in general, less connected to other sites (Henriques-Silva et al., 2019), and therefore tend to receive fewer settlers from the central pool of species present in a river basin (Henriques-Silva et al., 2019; Stegmann et al., 2019). The drainage network of the basin can also limit local dynamics of dispersal and colonisation (Brown et al., 2011), since the structural variables (physical and chemical) of headwater streams (branches) are different from those of larger downstream reaches (mainstems) (Brown et

al., 2011; Vannote et al., 1980). These differences limit the movement of certain species between small-order streams (Brown et al., 2011; Fagan, 2002). Thus, the dendritic configuration of the drainage network can act as a barrier to the movement of species with low dispersal capacity (Heino, Melo, et al., 2015; Heino, Nokela, et al., 2015; Palheta et al., 2021; Vitorino Júnior et al., 2016).

Local environmental variables (e.g. width, depth, current velocity, substrate and canopy cover) are responsible for fish richness and abundance (Fernandes et al., 2013; Leitão et al., 2018; Mendonça et al., 2005). However, these local variables (which operate at the site level) are controlled by catchment-scale variables (e.g. geology, climate and the vegetation structure of the river basin) (Benone et al., 2017; Frissell et al., 1986; Leal et al., 2016). Thus, the influence of environmental processes (i.e., niche-based) in the structuring of fish assemblages operates at different spatial scales (Benone et al., 2020; Hoeinghaus et al., 2007; Macedo et al., 2014; Paller et al., 2016).

The new frameworks proposed for analysing metacommunity dynamics (i.e., Leibold et al., 2021; Thompson et al., 2020) suggest that biotic interactions play a key role in the distribution of species in communities. The effects of these interaction processes are more evident in less diverse communities (Saavedra et al., 2017). It is not clear how biotic interactions influence the organisation of megadiverse communities in places with high environmental heterogeneity (e.g. ichthyofauna of Amazonian streams). However, local coexistence theories establish that interspecific interactions take place when organisms affect the availability of resources common to different taxa (e.g. space and nutrient availability) (Adler et al., 2018; Chesson, 2000). *Terra-firme* forest streams in the Amazon are considered stable aquatic environments, since they are not subjected to the remarkable seasonal inundations typical of larger river-floodplain systems (Junk et al., 1989). However, during the rainy season, Amazon forest streams can experience a predictable higher frequency of storms and short-term floods (Borba et al., 2021; Espírito-Santo & Zuanon, 2017). That way, it is expected that, in headwaters, great hydrological variation together with high environmental heterogeneity (Mendonça et al., 2005; Zbinden & Matthews, 2017) should make biotic interaction processes less frequent.

In this context, we examined how environmental conditions (at sites and at the basin scale), drainage network structure, spatial autocorrelation and interspecific interactions contribute to fish metacommunity dynamics in *terra-firme* Amazonian streams. Initially, due to differences in the niches of species in these communities, we postulate that (H1) *environmental conditions (at sites and at the basin scale) and the structure of the*

drainage network should influence the presence and abundance of fish species in terra-firme streams. Additionally, we expect dispersal processes to explain part of the variation in the structure of local assemblages, as the drainage network limits dispersal and local colonisation dynamics. Thus, we postulate that (H2) *the spatial (hydrographic) distance within a river basin should create dissimilarity in fish assemblages in upland streams.* Finally, we expect (H3) *that high environmental heterogeneity and dispersal restrict interspecific interactions in terra-firme Amazonian streams,* resulting in a low effect of these interactions on spatial co-occurrence among species.

Methods

Study area

This study was conducted in *terra-firme* streams situated in the Eastern Brazilian Amazon, specifically in the region of Volta Grande do Xingu (Figure 1 and Figure S1). The study area lies within a geologic transition zone, featuring sediments from both the craton and the Amazon sedimentary basin (Sawakuchi et al., 2015). The region has a tropical, hot, and humid climate, with an average air temperature of 26°C (Ghilardi & Camargo, 2009). The basin's average annual precipitation is 1963.5 mm, with the study region experiencing a rainy season from December to May, and a dry season from June to November (Santos et al., 2016).

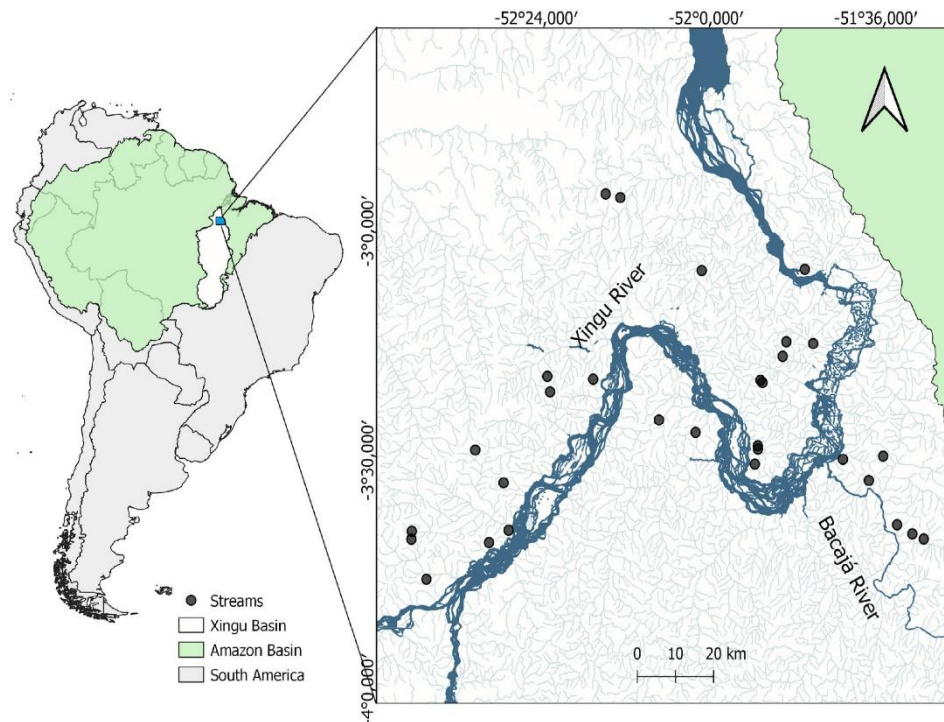


FIGURE 1 Geographic location of 30 streams sampled between March 2012 and October 2014 in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon.

Data acquisition

Environment and fish sampling

We collected environmental data and fish samples from 30 stream plots (1st and 2nd orders in the Strahler scale) (Figure 1; Table S1). Each plot was sampled during both the rainy (January–April) and dry (June–October) seasons, yielding a total of 60 samples. Field activities took place between March 2012 and July 2014 (Table S1). Data collection adhered to the protocol proposed by the Projeto Igarapés (<https://ppbio.inpa.gov.br/sites/default/files/Peixes.pdf>) (Mendonça et al., 2005). This methodology, which evaluates both the local fish assemblage and the physical–chemical features, has been extensively employed in Amazon streams (Borba et al., 2021; Dias et al., 2010; Mendonça et al., 2005; Rodrigues-Filho et al., 2018; Stegmann et al., 2019). According to the protocol, a plot represents a 50-meter section of a stream. During each sampling event, we recorded the average width (m) and depth (m) of the streams using six measurements in equidistant transverse transects along the plot. Mean canopy cover (%) was estimated based on 5 b/w photographs of the canopy. We measured five physicochemical variables – electrical conductivity (mS/cm), pH, dissolved oxygen (mg/L), saturated oxygen (%), and water temperature (°C) — using a multiparameter probe (YSI 556) at each plot's centre (Table S2). We also documented the relative composition of the substrate by sampling five equidistant points in six cross-sections along the plot. The relative composition of the substrate (%) was estimated based on the frequency of nine material categories: clay, sand, trunk (wood with a diameter larger than 10 cm), litter (composed of leaves and small branches), fine litter (fine particulate matter), root (tangle of mostly fine roots from marginal vegetation), aquatic plants, rocks and gravel (Table S3).

For fish collection, we blocked the ends of each plot with fine mesh nets (5 mm between opposite nodes). Three people explored the stream's section using dip nets, small seine nets, and sieves to capture fish over 2 h or until no fish were seen when moving along the stream. To facilitate capture and increase our sampling effort, we employed four additional nets to further divide the plots into 10-meter segments. After collection, fishes were euthanized with a lethal dose of Eugenol, fixed in a 10% formalin solution, and subsequently

sorted, counted, and identified to the species level using taxonomic keys (later confirmed by specialists).

Catchment-scale variables and drainage network structure

We employed the TauDEM5 tool (Tarboton, 2014) to construct the drainage network and delineate the catchment area using 30 m resolution satellite images (Shuttle Radar Topography Mission – SRTM), obtained from the EarthExplorer website (<http://earthexplorer.usgs.gov/>). The catchment area was defined with the outlet determined from the sampled point (Allan et al., 1997; Leal et al., 2016; Figure 2). We calculated the slope of the streams' catchment based on the SRTM images using QGIS (QGIS.org, 2021). We used land-use maps from project *MapBiomass* (<https://mapbiomas.org/en/colecoes-mapbiomas>; Souza et al., 2020) in order to calculate the percentage of forest cover (%) present in the catchment. Forest cover included: primary forest (undisturbed), and secondary forest (Areas that have been affected by fire or logging, forest resulting from natural succession processes, after total or partial suppression of primary vegetation by anthropogenic actions or natural causes, with remaining trees from primary vegetation possibly occurring) (Table S4).

For each sample site, we considered the main downstream stream as the largest stream (Strahler's order) that connects the sampling site to the main river (Xingu or Bacajá River) (Figure 2). Main streams ranged from 4th to 6th order in our dataset. Using this definition, we calculated the distance along the watercourses between the sample site and the main downstream stream. Additionally, we computed the distance (along the watercourses) between the sample site and the main downstream stream. We also calculated the total extension of the drainage network for each sample site, starting from the main river (Figure 2; Table S4).

We considered the distance to the mainstream as a measure of connectivity between the sample site and potentially similar environments without passing through significant environmental filters (i.e., the main river). This is supported by the fact that Amazonian stream assemblages typically have small-sized species with restricted distributions and limited ability to perform long migrations (Castro, 1999; Mendonça et al., 2005). Therefore, greater distances between the sample site and the mainstream indicate lower connectivity to the available environments within this drainage network. The distance to the main river (Xingu or Bacajá River) was used as a measure of the effect of large rivers on the structure of the ichthyofauna (Stegmann et al., 2019). Locations near large rivers are more connected to the central pool of species in the basin, whereas more distant environments are less

connected to this regional pool. The extension of the drainage network served as a proxy for the availability of environments without going through major environmental filters (i.e., the main river). Therefore, a larger extension of the drainage network represents a greater availability of environments for the ichthyofauna.

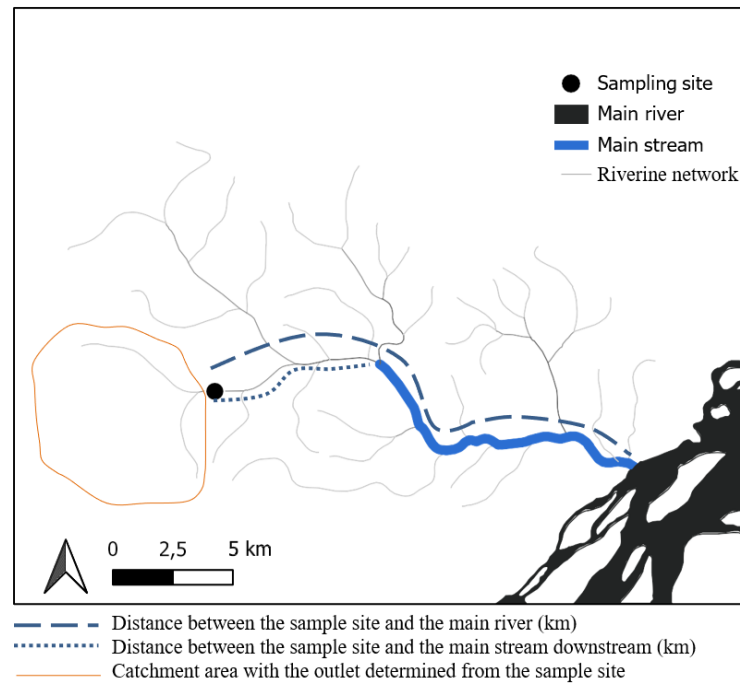


FIGURE 2 Scheme of how the drainage network structure variables were defined. Distance between the sampling sites and the main river (km). Distance between the sampled section and the mainstream downstream (km). Catchment area with the outlet determined from the sample site (km²).

Data analysis

Local environmental variables were subjected to a principal component analysis (PCA) to reduce the dimensionality of the data (Legendre & Legendre, 2012) (Supplementary S2). We selected the first three PCA axes, which accounted for 59% of the total variation (Supplementary S2). This left us with nine environmental variables of interest: PC1, PC2, PC3, catchment area (km²), catchment forest cover (%), catchment slope (%), an extension of the drainage network (km), distance from the mainstream (km) and distance from the river (km). However, as the distance from the river was correlated with the extension

of the drainage network ($r = .82$) and the distance from the mainstream ($r = .78$), we excluded it from subsequent analyses. Our predictor matrix then consisted of eight variables.

We employed the Hierarchical Modeling of Species Communities (HMSC) framework (Ovaskainen et al., 2017; Tikhonov et al., 2020) to fit a Joint Species Distribution Model (JSDM) with Bayesian inference (Warton et al., 2015). The HMSC framework uses environmental predictors as fixed effects and spatiotemporal variables or hierarchies as random effects to make community-level inferences (Ovaskainen et al., 2017; Tikhonov et al., 2020). This way, the model estimates the responses of all species (presence or abundance) simultaneously (Ovaskainen et al., 2017). All variation not explained by fixed factors and random effects (i.e. residual variation) in the HMSC can be used to infer species co-occurrence patterns that do not result from their shared responses to the environmental covariates (fixed effects) in the model (Ovaskainen et al., 2017).

To construct the JSDM model, we excluded rare species (found in less than 10% of streams) to prevent an excessive increase in the importance of the model's covariates (Ovaskainen & Abrego, 2020). Our model used the abundance of 45 species with a Poisson distribution as a response variable. Environmental variables were considered fixed effects, and geographic coordinates (spatially explicit) and sample size (sampling scheme) were considered random effects. We were not interested in the temporal effect on fish community structure. However, in an exploratory model, we included the explicit temporal effect (dry and rainy season) as a random factor, as allowed in HMSC. In this exploratory data analysis, temporal structure accounted for less than 1% of the variation. A PERMANOVA analysis (species abundance [Bray-Curtis]: pseudo- $F_{1,60} = 1.43$, $p = .100$) revealed that the fish assemblage composition of the streams did not differ between seasons. The HMSC was performed using the Hmsc-R package (Tikhonov et al., 2020) with five Markov Monte Carlo chains, each with 1000 samples. In this process, all five chains were sampled, with 2,000,000 interactions per chain. We discarded the first 150,000 samples of each chain as potentially transient and diluted the remaining ones by 1850, resulting in 1000 additional samples per chain. Model convergence was evaluated based on the effective size of the subsequent sample and the Gelman-Rubin convergence diagnostic for Beta (β) and Omega (Ω) values (Tikhonov et al., 2020). We assessed model fit by comparing the pseudo- R^2 of explanatory (before cross-validation) and predictive (after cross-validation) power using twofold cross-validation.

To test our hypotheses, we evaluated different aspects of the constructed model. To assess H1, we partitioned the variance in abundance explained by environmental variables and by random effects of data sampling (spatial autocorrelation and collection site). We also

analysed the β parameter for combinations of species and environmental variables to determine whether positive or negative relationships exist.

To test H2, we investigated the effect of increasing hydrographic distance on the dissimilarity of fish assemblages from two perspectives: one where the increase in community dissimilarity reflects dispersal limitation directly due to increasing distance; and a second where it is due to differences in environmental conditions at increasing spatial scales. To distinguish between these possibilities, we predicted species abundance using our trained model. We initially applied the Hellinger transformation to the predicted values of species abundances (Legendre & Gallagher, 2001). Using the predicted values, we calculated the Bray–Curtis dissimilarity index for all paired samples (Faith et al., 1987). We then performed a multiple regression on distance matrices (MRM) (Legendre et al., 1994; Lichstein, 2007), using the predicted paired dissimilarity and paired spatial distance (km; hydrologic distance). We performed a regression using the dissimilarity predicted based on the full species distribution model (including all environmental variables) and another regression with the dissimilarity calculated based on the same model but controlling for the effect of the environment. To control for the effect of the environment, all environmental variables (fixed effects) were adjusted to their mean. For our study group and environment, we expect that both models will be affected by the increase in distance. However, we anticipate that the complete model, which includes all environmental variables, will be better at explaining the variation in the data (measured by R^2) because it considers both the effect of distance and changes in environmental conditions. In contrast, in some cases where the increase in community dissimilarity is only due to dispersal limitation resulting from extreme dispersal distances, and not due to differences in environmental conditions at increasing spatial scales, we expect the complete model to have less explanatory power.

Finally, to verify H3, we evaluated the effects of interactions between species through residual correlations, after controlling for environmental variables. To this end, we present a co-occurrence matrix of the pairs of species that co-occurred more or less frequently than what was predicted by the correlation modelled using the explanatory variables (Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017).

Results

Community description

We identified 7954 fishes, representing 89 species, 26 families and eight orders (Table S5). Fifteen species were, on average, registered per stream (range = 3–32, s.d. = 8.4). Twenty-seven species made up 90% of captured specimens, and the sum of the 10 most abundant species represented 70% of all fish collected. The 10 most abundant species were *Knodus* aff. *savannensis* (24.4%), *Copella arnoldi* (13.4%), *Moenkhausia oligolepis* (7.5%), *Hemigrammus* sp. “collettii” (5.5%), *Astyanax* aff. *bimaculatus* (3.9%), *Moenkhausia celibela* (3.6%), *Phenacogaster* aff. *napoatilis* (3.5%), *Hyphessobrycon juruna* (3.5%), *Aequidens tetramerus* (3.3%) and *Apistogramma* sp. (2.1%). No species was recorded in all sampled streams. Still, 23 species occurred only in a single stream, and 45 species occurred in three or more streams. The three most frequent species were present in 22 out of 30 sampled streams (*Astyanax* aff. *bimaculatus*, *Moenkhausia oligolepis* and *Hoplias malabaricus*; Table S5).

Stream characteristics

The streams studied in the Eastern Brazilian Amazon had slightly acidic waters (mean pH 6.4, range = 4.4–8.7), with low conductivity (mean = 0.31 $\mu\text{S}/\text{cm}$, range = 0–2.7) (Table S2). The average water temperature was 25.85°C (range = 22.8–30.1) and the average dissolved oxygen level was 6.59 mg/L (range = 1.15–9.72). The average channel depth was 0.2245 m (range = 0.047–0.558) and the average channel width was 2.3325 m (range = 0.917–4.88). The average canopy cover in the streams was 69.56% (range = 1.09–93.83). The stream bottom predominantly covered by mainly covered by sand (mean = 35.1%, range = 1.6–88.7), banks of fine litter (mean = 15.4%, range = 0.0–77.7) and the coarse litter (mean = 15.4%, range = 0.0–47.0) (Table S3).

The average catchment area was 3.4 km² (range = 0.25–17.2 km²) and average catchment slope was 11.4% (range = 4.3%–20.8%) (Table S4). The average forest cover in the catchment of the streams was 49.6% (range = 0.15%–100%). The average extension of the drainage network was 373.2 km (range = 7.35–1482.7 km), and the average distance from the mainstream was 6.9 km (range = 0.13–23.1 km) (Table S4).

The first three axes of the PCA (Supplementary S2), which were used in the construction of the JSDM model, summarised 62.38% of the variation in local environmental factors. The first component (PC1) accounted for 26.2% of the variance in the factors. The

highest loadings on this component were positively associated with structural and limnological characteristics of the streams (dissolved oxygen, channel depth, conductivity) and negatively associated with the presence of fine litter. The second component (PC2), comprising 21.9% of the variance, was positively associated with water temperature and aquatic plants, and negatively associated with coarse litter and canopy cover. The third component (PC3), with 13.3% of the variance, showed a positive relationship with sand and a negative relationship with fine litter and channel depth.

Model convergence and fit

Model fit results summarised by MCMC convergence diagnostics for the estimated parameters based on effective sample size and scale factor are considered satisfactory. The potential scale reduction factors for the beta-parameters (responses of species to environmental covariates) were on average 1.14 and potential scale reduction factors for the omega-parameters (species associations) were on average 1.32 (Figure S2). Our model showed a good fit to the data with mean RMSE = 2.46 and mean pseudo- $R^2 = .34$, with predictive power being lower than explanatory power, indicating good model performance (Table S6). The highest coefficients of discrimination (pseudo- R^2) were observed for *Knodus* aff. *savannensis* (0.89) and *Aequidens tetramerus* (0.65), and the lowest for *Phenacorhamdia* sp. (0.09) and *Hyphessobrycon copelandi* (0.10) (Table S6).

Variance partitioning

The greater variance in species abundances was attributed to fixed rather than the random effect of streams (Figure 3, Table S7). Local environmental variables explained an average of 27.2% of the variation, with PC1 accounting for 10% of this variation, followed by PC2 (mean = 9%) and PC3 (mean = 7.2%) (Table S7). Basin-scale variables explained on average 25.2% of the variation in species abundance, with the average slope of the catchment accounting for almost half of the variation. Drainage network structure variables explained on average 21.7% of the observed variation in species abundances, with drainage network extension explaining on average 12.5% and distance to the mainstream 8.3% of the variation. (Figure 3, Table S7).

Random effects (sampling location and spatial autocorrelation) explained on average 25.8% of the variation (Figure 3, Table S7). Sampling location explained on average 12.9%

of the variation. Spatial autocorrelation explained 12.9% of the mean-variance in species abundances.

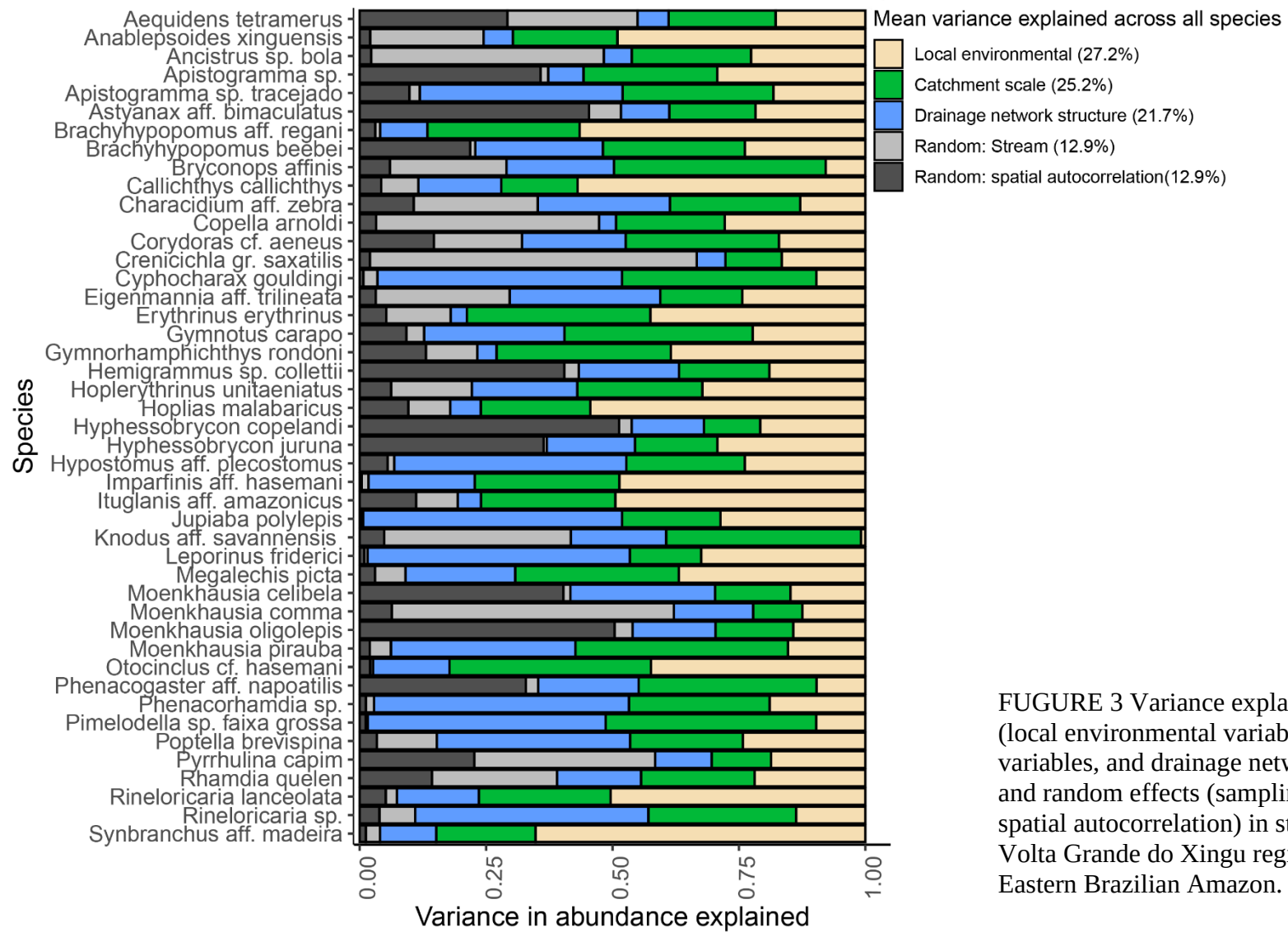
Based on inspection of the β parameters that estimate the relationships between environmental covariates and species abundances (Figure 4), no fish species showed a relationship with all variables used in the model. Most species (68%) exhibited significant responses to the PC1 variable, with eight species showing a positive response (increase in abundance with higher PC1 values) and 23 species showing a negative response (decrease in abundance with higher PC1 values). Additionally, 17 species responded positively to the average slope of the catchment and 12 species responded negatively to this variable. Regarding the structure of the drainage network, 13 species responded negatively to the distance to the mainstream and 14 species responded negatively to higher values of the drainage network (Figure 4).

Spatial connectivity

For abundances predicted based on the complete model, dissimilarity ranged from 0.19 to 0.98 (mean = 0.62, s.d. = 0.16). Dissimilarity values for communities predicted based on the model that disregarded environmental conditions ranged between 0.137 and 0.72 (mean = 0.45, s.d. = 0.11). Paired dissimilarity values were reduced when the effect of the environment was removed. Community dissimilarity increased together with spatial distance for the abundance values predicted based on the full model (MRM: $R^2 = .21$, $p = .001$) (Figure 5). Even with reduced dissimilarity values, when we removed the effect of the environment, community dissimilarity also increased together with spatial distance (MRM: $R^2 = .10$, $p = .021$) (Figure 5).

Interspecific interactions

We detected only four positive associations in which species co-occurred more frequently than expected by chance or due to environmental filtering. *Gymnorhamphichthys rondoni* positively co-occurred with *Copella arnoldi* and *Erythrinus erythrinus*. *Copella arnoldi* co-occurred with *Erythrinus erythrinus* and *Hyphessobrycon copelandi* with *Moenkhausia oligolepis* more frequently than expected by chance. The only negative association detected was between *Moenkhausia comma* and *Erythrinus erythrinus*.



FUGURE 3 Variance explained by fixed (local environmental variables, basin-scale variables, and drainage network structure) and random effects (sampling location and spatial autocorrelation) in streams in the Volta Grande do Xingu region, Pará state, Eastern Brazilian Amazon.

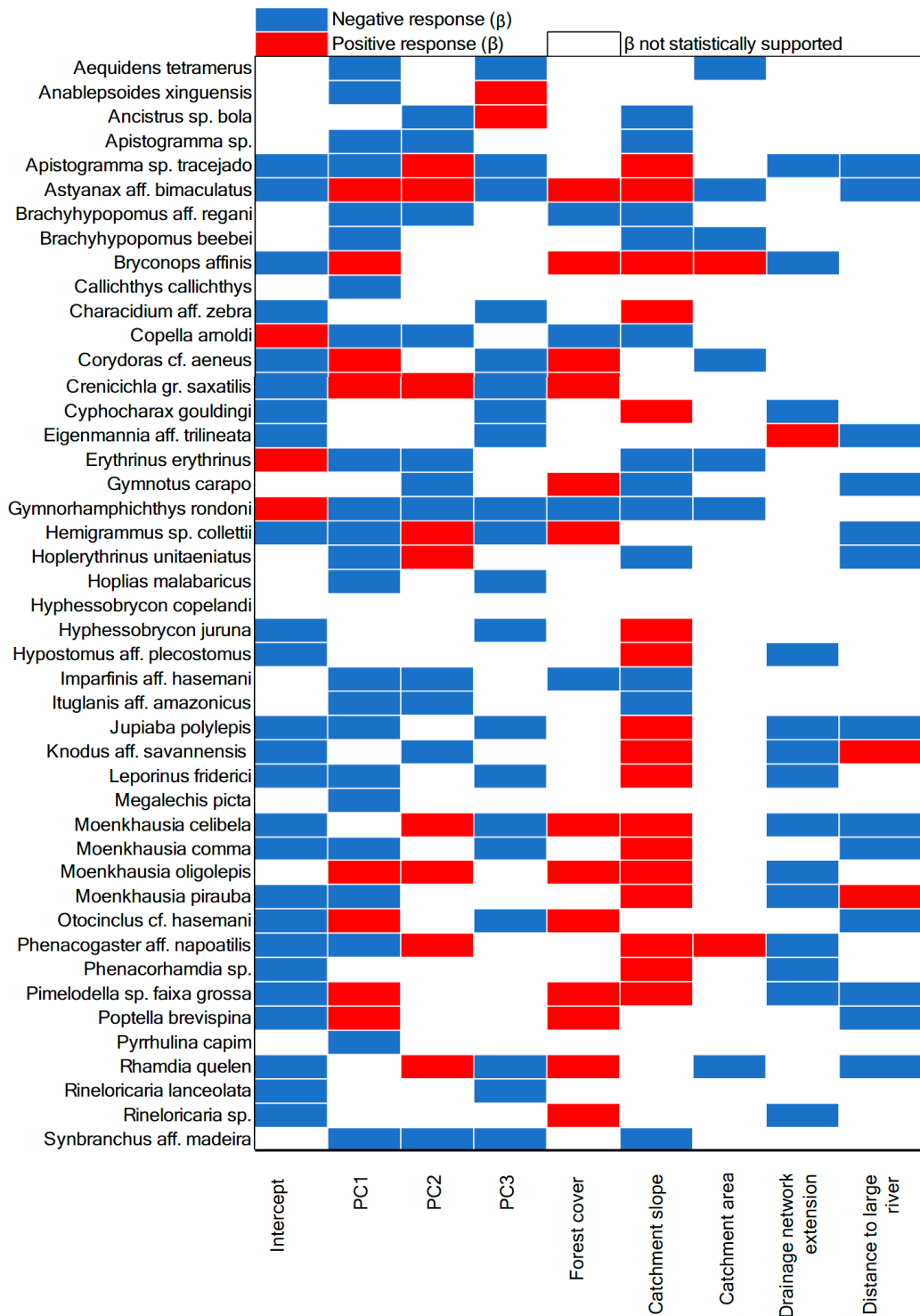


FIGURE 4 Heat plot summarising responses to all environmental covariates in the joint species distribution model (CI=95%). Red cells indicate positive responses (abundance increases as the values of the environmental covariate increase), while blue cells indicate negative responses (abundance decreases as the value of the environmental covariate increases).

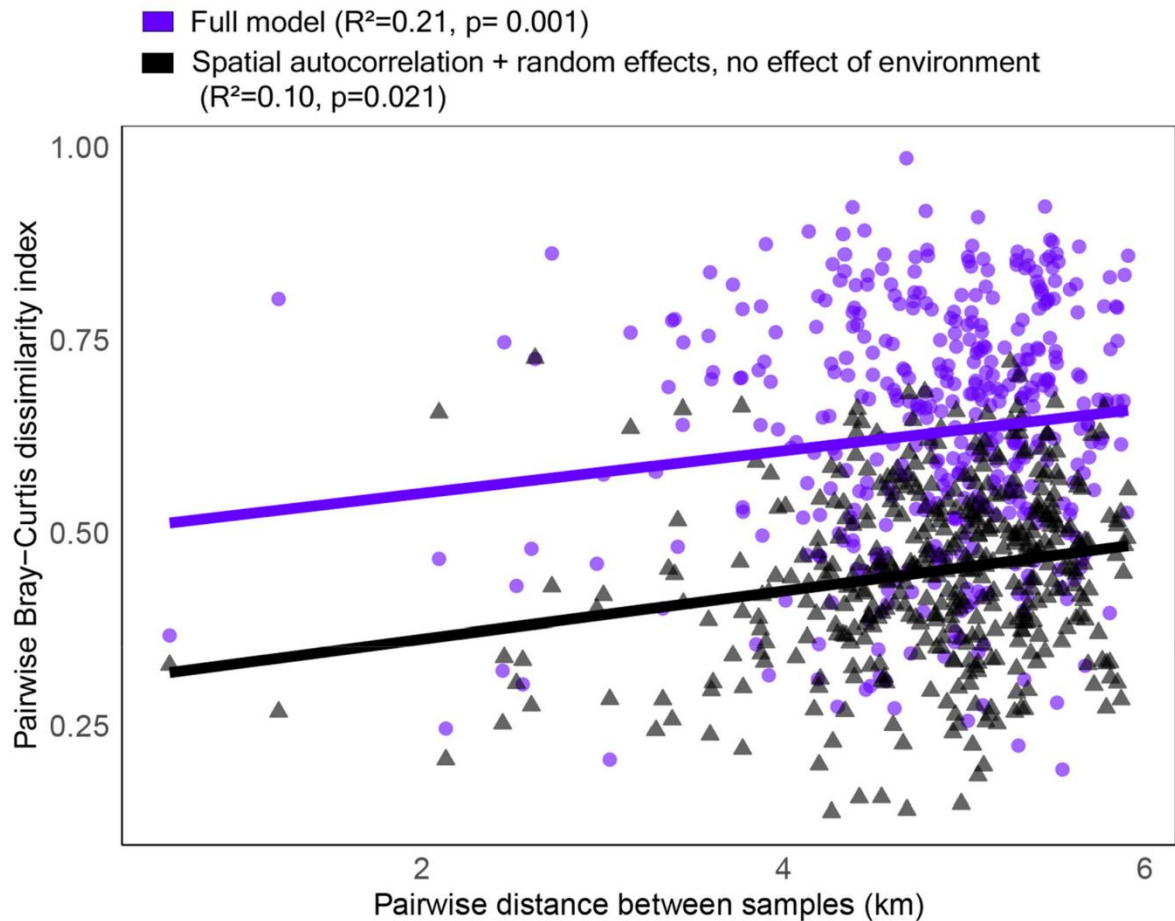


FIGURE 5 Bray-Curtis dissimilarity index as a function of spatial (hydrographic) distance between each combination of sampled streams. Blue dots show the pairwise dissimilarity predicted by the complete Joint Species Distribution Model (JSDM), using environmental and spatial data. Black triangles show the pairwise dissimilarity predicted by the JSDM without the effect of the environment (environmental variables were set to their mean values).

Discussion

We sought to evaluate the contribution of environmental factors, dispersal, and interspecific interactions on fish metacommunity dynamics in terra-firme Amazonian streams. Our findings indicate that environmental conditions and dispersal limitations play a major role in shaping the distribution and dynamics of fish species in these systems. Few species were found coexisting that could not be explained by spatial structure or shared responses to the environment, suggesting that interspecific interactions have minimal influence. Our results are consistent with previous studies that have highlighted the importance of environmental conditions and dispersal limitations for explaining stream fish metacommunity structure (Benone et al., 2018; Mozzaquattro et al., 2020; Palheta et al., 2021).

The role of environmental and spatial factors in the organisation of aquatic metacommunities depends on taxonomic groups (Schmera et al., 2018) and spatial scale (Brown & Swan, 2010; Heino, Melo, et al., 2015; Heino, Nokela, et al., 2015). Specifically for stream ichthyofauna, in small and intermediate areas, the structuring of the metacommunity is predominantly influenced by environmental factors (Heino et al., 2012). However, in larger extensions, the limitation of dispersion becomes a more relevant factor in determining observed patterns (Muneepeerakul et al., 2008). In the studied stretch of the Xingu River basin, we found support for the limitation of dispersal and environmental filtering. With an average distance of 152 km (range = 1.83–367 km) among the analysed streams, spatial autocorrelation explained part of the variance in species abundance. Additionally, distance (hydrographic) explained the increase in community dissimilarity. Moreover, our model's explanatory power increased when we related dissimilarity with distance while maintaining the effect of the environment.

Environmental variables (local and at the basin scale) and the structure of the drainage network explain most of the variation in fish species composition. These results can be explained by the effect of resource availability and habitat quality in determining the species composition of stream fish (Anjos, 2013; Espírito-Santo et al., 2009; Hoeinghaus et al., 2007; Matthews, 1998; Mendonça et al., 2005), reinforcing the effect of niche-based processes in structuring headwater stream communities (Brown & Swan, 2010; Winegardner et al., 2012; Zbinden & Matthews, 2017). Small Amazonian forest streams are generally highly oligotrophic systems, where the main source of energy is of allochthonous origin (Anjos, 2013). Thus, greater canopy coverage and greater amounts of coarse and fine litter should increase the availability of resources for local species (e.g., food and shelter). Omnivorous and insectivorous species dominate the composition of fish assemblages in streams where energy can be directly obtained through the consumption of terrestrial insects, litter-associated invertebrates and detritus that fall into the water (Brejão et al., 2013; Anjos, 2013; Sabino & Zuanon, 1998).

At the basin scale, catchment slope (mean = 11.41%, range = 4.32%–20.81%) was the variable that best explained the variation in the distribution of fish species. The slope of the stream has no direct influence on fish species (Camana et al., 2016; Mozzaquattro et al., 2020). Slope, however, directly influences other characteristics of local habitats, such as flow, hydrological disturbances (e.g., flash floods) (Camana et al., 2016) and substrate heterogeneity (Benone et al., 2017), which are in turn key factors in the organisation of ichthyofauna in terra-firme Amazonian streams (Borba et al., 2021; Espírito-Santo et al.,

2009; Mendonça et al., 2005). Headwater streams are strongly influenced by local rainfall (Borba et al., 2021; Espírito-Santo et al., 2009), where sudden events of high flow are common throughout the year due to high precipitation. Streams with steeper slopes also become more prone to these sudden high-flow events, resulting in more hostile environments in terms of flow velocity (Resh et al., 1988). The abrupt changes in these environments should partly explain the relationship between slope and ichthyofauna observed in our results. Among the species whose abundance was related to the slope of the catchment, active swimmers that occupy the middle and upper layers of the stream channels (e.g., *Cyphocharax gouldingi* and *Bryconops affinis*) showed a positive response to increasing steepness. This positive relationship can be explained by the high swimming capacity of these species, which can more efficiently search for shelters during periods of high flow. Conversely, most species that showed negative responses to steeper slopes (e.g., *Gymnorhamphichthys rondoni* and *Ituglanis aff. amazonicus*) have limited swimming capacity.

Estimated β parameters suggest that the larger the drainage network, the lower the abundance of most species that presented responses to this variable (14 out of 15). These results suggest that, even on a smaller scale, the dendritic configuration of the drainage network may be acting as a barrier to the movement of fish species (Heino, Melo, et al., 2015; Heino, Nokela, et al., 2015; Palheta et al., 2021; Vitorino Júnior et al., 2016). Headwater streams are, in general, less connected sites (Henriques-Silva et al., 2019), receiving fewer settlers from the central pool of species present in the basin (Henriques-Silva et al., 2019; Stegmann et al., 2019). However, it is important to highlight that our inferences are based on an analysis focused on the most common species. Rare species, recorded in less than three of the 30 sampled streams, were removed from our model in order to avoid an overestimation of the importance of the model's covariates (Ovaskainen & Abrego, 2020). It is possible, then, for these species to be influenced by the extension of the drainage network in an opposite way. We used the extension of the drainage network as a proxy of the connectivity between our sampled streams and the main river. Thus, the effect of drainage network size may be more important than our analysis suggests, because Amazonian forest streams have many small-sized species with restricted distributions and limited migration capacity (Castro, 1999; Mendonça et al., 2005); therefore, a drainage network more extensively connected to the main river (which may act as a barrier) might be key in the maintenance of these species.

Our results indicate that interspecific interactions have a minimal influence on the distribution and dynamics of fish species in these systems. We observed few species co-occurring in the studied streams (co-occurring more than predicted by their correlation

modelled by the environmental characteristics of streams). Our results confirm the initial inferences of Peres-Neto (2004) that the high heterogeneity of neotropical streams may reduce the importance of biotic interactions in the dynamics and distribution of fish communities in these ecosystems. An inclusion of biotic interactions as one of the key factors in the organisation of metacommunities (Leibold et al., 2021; Thompson et al., 2020) is based on the concepts of local coexistence theories, which establish that interspecific interactions occur when organisms affect the availability of resources that are common to different taxa (e.g., space, nutrient availability) (Adler et al., 2018; Chesson, 2000). Therefore, the high environmental heterogeneity of streams (Meyer et al., 2007) together with the dendritic characteristics of the drainage network (Brown et al., 2011; Fagan, 2002) restrict interspecific interactions in terra-firme Amazonian streams. This set of factors would result in the segregation of species along an environmental and spatial gradient and lead to the absence of a regional pool of species corresponding to all analysed streams, reducing possible effects of interspecific interactions on the local dynamics of assemblages. We recognise that the usefulness of using the species associations for inferring the importance of species interactions is still debated (Blanchet et al., 2020). However, we believe that our results are significant in questioning the effects of interactions, which are often considered critical factors in the organisation of biological communities.

While this study focuses on the fish communities in terra-firme streams in the Eastern Brazilian Amazon, the findings have broader implications for understanding the role of environmental factors and interspecific interactions in shaping fish metacommunities in other stream systems. The high heterogeneity of neotropical streams may reduce the importance of biotic interactions in the dynamics and distribution of fish communities in these ecosystems. This may also be the case in other systems with high environmental heterogeneity and limited dispersal, such as some temperate headwater streams (e.g., Heino, Melo, et al., 2015; Heino, Nokela, et al., 2015). However, it is important to note that the specific environmental factors and species interactions that shape fish communities may vary depending on the system. Furthermore, it is still necessary to advance in understanding how different structural characteristics of lotic environments can influence the effect of biotic interactions on the dynamics of communities. For example, in terms of floodable mainstem systems, the flood pulse in these systems may create opportunities for dispersal and colonisation, which could increase the importance of interspecific interactions in shaping fish communities.

Incorporating the effects of temporal factors in metacommunity studies may be essential to recognise the processes responsible for metacommunity dynamics (Guzman et

al., 2022). Previously, for the streams analysed in the Xingu River basin, it was observed that those with lower environmental variability had greater structural stability of the ichthyofauna, but environmental disturbances, such as intense droughts, can alter the composition of fish and these changes may persist in the midterm (Martins et al., 2022). Here, we isolated the effect of temporal structure in our analyses. Future research should focus on understanding the relative importance of biotic, environmental, and spatial interactions in metacommunity structure through temporal data series.

In general, we observed the combined action of environmental factors (at multiple scales), the structure of the drainage network and spatial autocorrelation in the organisation of fish assemblages in terra-firme streams in the Amazon. Our results corroborate our hypotheses that the environmental conditions at multiple scales, the structure of the drainage network and the spatial (hydrographic) distance within a river basin induce dissimilarity in fish assemblages in terra-firme streams. Furthermore, few species were frequently found coexisting that could not be explained by spatial structure or shared responses to the environment. This low number of biotic interactions is likely attributed to dispersal limitation, partly due to the structure of the drainage network, and the high heterogeneity of environmental conditions. These factors may be contributing to a weaker impact of biotic interaction processes on the dynamics of fish metacommunities in small terra-firme Amazonian streams.

Author contributions

This research was conceptualised by ARM and LUH. The methods were developed by DAB, LMS and TG. ARM and DAB conducted field work and lab analyses. ARM and LUH analysed the data. ARM prepared the figures and tables. ARM and LUH interpreted the results. The research was carried out with input from all authors. Writing was led by ARM and LUH and all other authors contributed to review and editing.

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Conflict of interest statement

The authors declare that they have no conflict of interest.

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Supplement materials

Table S1 Date of sampling events of the 30 streams sampled in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon.

Stream	Rainy season	Dry season	Time in months between sampling events
stream01	March/April 2012	June/July 2012	3
stream02	March/April 2012	June/July 2012	3
stream03	March/April 2012	July 2013	15
stream04	March/April 2012	October 2012	6
stream05	March/April 2012	July 2013	15
stream06	March/April 2012	June/July 2012	3
stream07	March/April 2012	June/July 2012	3
stream08	March/April 2012	June/July 2012	3
stream09	March/April 2012	June/July 2012	3
stream10	March/April 2012	June/July 2012	3
stream11	March/April 2012	June/July 2012	3
stream12	March/April 2012	June/July 2012	3
stream13	March/April 2012	June/July 2012	3
stream14	March/April 2012	September 2012	5
stream15	March/April 2012	June/July 2012	3
stream16	March/April 2012	July 2013	15
stream17	March/April 2012	June/July 2012	3
stream18	March/April 2012	June/July 2012	3
stream19	March/April 2012	June/July 2012	3
stream20	March/April 2012	June/July 2012	3
stream21	March/April 2012	June/July 2012	3
stream22	January 2013	June/July 2012	6
stream23	January 2013	June/July 2012	6
stream24	January 2013	July 2013	6
stream25	January 2013	June/July 2012	6
stream26	January 2013	June/July 2012	6
stream27	January 2013	July 2013	6
stream28	March 2013	June/July 2012	8
stream29	January 2014	June/July 2012	18
stream30	March 2014	July 2014	4

Table S2 Local variables values of 30 stream plots in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon.

Stream	Season	Temperature (°C)	Water conductivity (mS/cm)	pH	Dissolved oxygen (mg/L)	Mean depth (m)	Mean width (m)	Mean canopy cover (%)
stream01	Rainy	24.43	1.49	7	8.85	0.27	4.29	88.2
stream02	Rainy	25.08	1.46	7.02	8.76	0.41	4.88	75.98
stream03	Rainy	24.07	0.9	6.69	9.3	0.25	3.66	87.82
stream04	Rainy	28.39	1.25	6.67	7.53	0.39	2.96	29.46
stream05	Rainy	25.56	0.55	6.34	8.81	0.21	1.88	90.06
stream06	Rainy	25.16	1.08	6.22	9.22	0.51	2.48	81.14
stream07	Rainy	25.69	0.76	5.77	8.56	0.49	2.32	11.65
stream08	Rainy	26.55	0.25	5.78	7.8	0.32	3.2	4.57
stream09	Rainy	25.57	1.27	5.58	8.4	0.56	4.2	81.02
stream10	Rainy	25.58	0.98	5.59	8.72	0.45	2.73	88.62
stream11	Rainy	24.65	0.6	6.91	9.7	0.17	2.1	90.56
stream12	Rainy	25.12	0.48	6.66	9.22	0.21	2.8	93.46
stream13	Rainy	24	0.56	6.53	9.21	0.39	2.5	93.83
stream14	Rainy	26.23	0.02	6.11	5.05	0.11	2	91.94
stream15	Rainy	29.09	0.6	7.13	7.18	0.3	1.2	5.27
stream16	Rainy	24.37	0.35	6.7	9.72	0.13	2	92.65
stream17	Rainy	25.27	0.41	6.62	8.91	0.12	1.7	93.63
stream18	Rainy	27.09	0.57	6.92	8	0.26	1.5	20.41
stream19	Rainy	26.79	0.2	5.07	7.55	0.25	3	23.42
stream20	Rainy	25.75	0.18	5.13	9.21	0.29	2.52	86.99
stream21	Rainy	28.97	0.73	5.27	6.6	0.31	2.4	92.66
stream22	Rainy	24.4	0	6.08	6.97	0.08	1.84	89.1
stream23	Rainy	25.2	0.02	6.31	8.5	0.11	2.19	90.22
stream24	Rainy	24.9	2.7	5.71	7.45	0.15	2.17	88.65
stream25	Rainy	25.4	0	5.85	4.14	0.16	2.22	88.28

stream26	Rainy	26.2	0	5.75	5.46	0.22	2.88	84.3
stream27	Rainy	25.6	0.04	6.6	6.2	0.1	1.59	89.6
stream28	Rainy	27.3	0.02	5.58	6.1	0.41	4.2	82.85
stream29	Rainy	24.9	0.02	6.04	9.3	0.29	4.33	87.5
stream30	Rainy	25.1	0.04	6.14	6.5	0.09	2.57	87
stream01	Dry	23.8	0.07	7	5.47	0.08	2.07	82.21
stream02	Dry	24.4	0.11	7	6.72	0.19	2.26	60.26
stream03	Dry	26.5	0.11	6.81	6.5	0.15	3.57	79.88
stream04	Dry	29.5	0.16	6.91	5.8	0.25	2.9	29.93
stream05	Dry	30.1	0.04	4.43	4.4	0.1	1.58	78.1
stream06	Dry	22.8	0.05	7	7.59	0.18	1.92	72.14
stream07	Dry	28.2	0.05	7	7.31	0.25	1.68	29.85
stream08	Dry	27	0.02	6	7.27	0.09	1.48	1.09
stream09	Dry	27.1	0.06	7	5.87	0.28	3.35	55.19
stream10	Dry	25.4	0.05	7	5.73	0.27	2.35	71.46
stream11	Dry	24.1	0.01	8	4.51	0.09	1.75	79.7
stream12	Dry	28.8	0.01	8.7	1.22	0.18	1.63	80.29
stream13	Dry	23.5	0.02	7.81	4.48	0.3	2.3	83.39
stream14	Dry	24.3	0	6.28	5.84	0.34	1.33	70
stream15	Dry	27.9	0.12	5.62	7.7	0.37	1.19	2.77
stream16	Dry	23.6	0.02	5.95	3.8	0.06	0.96	89.69
stream17	Dry	24.5	0.06	6.5	3.29	0.09	1.4	81.25
stream18	Dry	26.2	0.03	6	1.15	0.17	1.03	330.95
stream19	Dry	28.5	0.01	7	3.9	0.22	2.13	13.19
stream20	Dry	29.2	0.01	7	7.01	0.22	2.32	67.9
stream21	Dry	25.9	0.1	7	6.1	0.13	1.56	77.98
stream22	Dry	25	0.01	7	8.81	0.25	0.92	72.67
stream23	Dry	24.6	0.04	7.05	4.21	0.13	1.3	82.76
stream24	Dry	25.8	0.02	6.35	5.5	0.13	2.28	87.49

stream25	Dry	26.5	0.02	6.27	4.95	0.14	1.8	80.33
stream26	Dry	23.2	0.02	5.37	5.42	0.22	3.2	85.16
stream27	Dry	27.1	0.07	6.41	5.9	0.18	1.71	86.95
stream28	Dry	23.5	0.06	7.41	1.97	0.19	2.25	76.94
stream29	Dry	26.6	0.02	6.71	8.17	0.2	4.07	66.03
stream30	Dry	24.8	0.03	6.41	2.2	0.05	1.38	87.32

Table S3 Substrate composition of 30 stream plots in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon.

Stream	Season	% Sand	% Clay	% Pebble/Gravel	% Coarse litter	% Fine litter	% Roots	% Rocks	% Wood	% Aquatic plants
stream01	Rainy	63.00	14.75	0.00	11.75	3.25	2.50	1.50	3.25	0.00
stream02	Rainy	61.50	6.75	0.00	16.00	3.00	7.50	0.25	4.00	1.00
stream03	Rainy	63.00	7.00	0.00	11.00	0.00	6.50	11.00	1.50	0.00
stream04	Rainy	45.00	5.50	0.00	10.00	0.50	3.00	34.50	1.50	0.00
stream05	Rainy	51.33	12.00	0.00	9.67	0.00	24.67	0.00	2.33	0.00
stream06	Rainy	22.00	0.75	0.00	5.00	0.00	3.50	54.75	14.00	0.00
stream07	Rainy	65.50	0.33	11.33	9.83	5.00	5.50	1.00	0.00	1.50
stream08	Rainy	73.05	20.50	0.00	1.35	0.25	3.00	0.00	1.75	0.10
stream09	Rainy	88.75	6.56	0.00	0.00	0.94	3.75	0.00	0.00	0.00
stream10	Rainy	18.33	0.00	0.00	1.00	1.33	0.00	10.33	67.67	1.33
stream11	Rainy	7.50	22.00	0.00	47.00	9.00	9.00	0.00	5.50	0.00
stream12	Rainy	45.00	14.00	0.00	30.00	1.00	9.00	0.00	1.00	0.00
stream13	Rainy	35.50	0.00	0.00	21.50	23.00	18.00	0.00	1.50	0.50
stream14	Rainy	34.50	1.50	2.00	35.50	21.00	5.50	0.00	0.00	0.00
stream15	Rainy	47.50	0.50	8.00	11.50	12.50	18.00	0.00	1.00	1.00
stream16	Rainy	49.17	0.67	0.00	6.83	41.33	0.00	0.00	0.00	2.00
stream17	Rainy	19.50	4.17	19.00	26.00	16.67	12.33	0.33	2.00	0.00
stream18	Rainy	30.00	1.00	0.00	1.33	61.67	0.00	0.00	0.00	6.00
stream19	Rainy	23.33	12.33	3.67	14.33	36.33	0.00	0.00	0.00	10.00

stream20	Rainy	62.17	2.50	9.33	7.33	3.50	2.17	0.33	12.33	0.33
stream21	Rainy	1.67	5.67	4.67	9.17	77.17	0.00	0.00	0.00	1.67
stream22	Rainy	30.50	1.50	45.00	0.00	4.00	17.50	0.00	0.00	1.50
stream23	Rainy	27.50	0.00	13.75	1.25	19.38	0.00	0.00	0.00	38.13
stream24	Rainy	25.00	2.00	6.50	27.00	19.00	20.50	0.00	0.00	0.00
stream25	Rainy	17.00	0.00	8.50	32.00	31.50	6.50	0.00	1.00	3.50
stream26	Rainy	30.63	0.00	2.50	8.75	8.75	31.88	0.00	1.88	15.63
stream27	Rainy	22.67	0.00	0.33	15.00	26.00	0.67	12.00	23.00	0.33
stream28	Rainy	60.50	2.00	0.00	24.00	0.50	13.00	0.00	0.00	0.00
stream29	Rainy	56.00	15.00	0.00	17.50	0.50	9.50	0.00	1.50	0.00
stream30	Rainy	13.00	13.00	62.00	5.00	1.00	5.00	0.00	1.00	0.00
stream01	Dry	34.33	1.00	18.83	19.17	19.00	2.33	0.00	5.33	0.00
stream02	Dry	13.33	2.67	41.33	15.67	16.83	1.00	3.00	5.50	0.67
stream03	Dry	26.40	0.00	0.00	3.20	6.80	0.40	63.20	0.00	0.00
stream04	Dry	23.67	4.00	2.33	19.50	9.33	11.67	9.00	17.67	2.83
stream05	Dry	64.00	22.40	9.20	0.80	0.00	3.60	0.00	0.00	0.00
stream06	Dry	5.17	0.00	27.33	7.00	11.33	3.67	40.67	3.83	1.00
stream07	Dry	44.33	1.00	14.83	24.83	9.50	4.33	0.17	1.00	0.00
stream08	Dry	38.00	0.33	0.17	6.83	30.33	6.17	0.00	1.00	17.17
stream09	Dry	34.17	1.00	18.00	6.33	19.17	4.67	0.00	0.67	16.00
stream10	Dry	18.17	2.83	2.33	2.00	5.50	0.67	64.83	2.67	1.00
stream11	Dry	7.50	10.33	5.33	23.00	41.83	2.00	0.00	8.00	2.00
stream12	Dry	14.33	9.67	12.83	24.17	23.00	4.00	0.00	12.00	0.00
stream13	Dry	15.33	5.40	0.00	31.43	23.67	12.67	0.00	11.50	0.00
stream14	Dry	12.67	17.33	3.00	28.83	21.17	6.67	0.00	10.33	0.00
stream15	Dry	27.00	8.17	7.50	22.00	9.83	16.17	0.33	9.00	0.00
stream16	Dry	23.50	3.17	5.00	29.17	21.00	8.17	0.33	9.67	0.00
stream17	Dry	12.00	0.00	2.00	41.33	32.00	3.00	0.00	9.67	0.00
stream18	Dry	78.40	0.00	0.40	9.20	3.60	8.00	0.40	0.00	0.00

stream19	Dry	20.00	0.00	0.33	32.33	25.33	12.33	0.67	9.00	0.00
stream20	Dry	46.17	4.67	4.83	21.83	11.00	4.17	0.00	7.17	0.17
stream21	Dry	6.00	5.17	0.33	42.83	33.00	7.50	0.00	5.17	0.00
stream22	Dry	40.40	0.00	25.60	22.00	8.00	4.00	0.00	0.00	0.00
stream23	Dry	13.00	8.67	25.33	2.00	25.33	11.50	0.00	0.00	14.17
stream24	Dry	79.60	0.00	3.60	6.80	5.60	2.40	2.00	0.00	0.00
stream25	Dry	15.00	3.00	4.50	35.50	23.67	10.33	0.00	8.00	0.00
stream26	Dry	5.50	0.00	22.17	9.17	36.17	12.83	0.00	1.83	12.33
stream27	Dry	74.00	0.00	14.00	4.80	5.60	0.40	1.20	0.00	0.00
stream28	Dry	59.67	4.17	0.17	7.00	4.33	5.67	0.00	1.67	17.33
stream29	Dry	57.00	3.17	12.17	5.50	3.83	12.83	0.00	2.83	2.67
stream30	Dry	7.67	0.33	58.17	2.83	11.33	5.67	11.17	0.00	2.83

Table S4 Geographic coordinates of sampled sites and catchment-scale variables and drainage network structure of 30 stream plots in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon.

Stream	X	Y	Forest cover (%)	Catchment slope (%)	Catchment area (km ²)	Extension of the drainage network (km)	Distance from the main stream (km)	Distance from the river (km)
stream01	-3.7597	-52.659	94.31	19.06	17.16	470.58	7.87	11.28
stream02	-3.6725	-52.694	99.67	13.72	12.86	470.58	19.95	23.29
stream03	-3.6551	-52.693	56.24	18.31	1.98	470.58	22.89	26.28
stream04	-3.5493	-52.477	17.1	14.1	1.58	67.02	1.45	7.4
stream05	-3.6531	-52.465	0.16	13.85	0.89	753.76	1.2	1.5
stream06	-3.4776	-52.543	19.3	13.39	2.17	860.47	23.09	32.47
stream07	-3.351	-52.367	21.25	13.79	2.08	895.03	12.41	33.04

stream08	-3.3172	-52.374	16.26	14.72	2.19	895.03	7.41	28.07
stream09	-3.4391	-52.025	38.35	14.94	12.65	66.81	1.45	7.72
stream10	-3.412	-52.111	32.92	20.81	3.12	162.46	7.25	13.13
stream11	-3.5083	-51.885	87.38	9.23	0.82	11.62	1.59	1.92
stream12	-3.4754	-51.878	77.2	11.4	1.81	45.85	3.02	5.81
stream13	-3.4686	-51.878	46.11	12.64	4.93	45.85	3.37	6.16
stream14	-3.2413	-51.811	35.16	13.36	0.9	141.95	3.9	16.77
stream15	-3.2453	-51.747	7.43	9.14	0.57	137.98	0.63	5.65
stream16	-3.3305	-51.867	99.45	7.68	0.55	232.93	11.66	19.59
stream17	-3.3252	-51.872	75.81	5.96	0.25	67.96	2.21	12.29
stream18	-3.2731	-51.819	44.29	8.95	0.7	110.73	4.6	12.98
stream19	-2.9188	-52.236	28.14	6.92	7.82	1482.7	19.36	38.06
stream20	-2.9265	-52.202	3.51	9.75	3.05	1482.7	2.99	29.87
stream21	-3.0861	-52.01	0.15	10.46	1.38	1224.27	7.15	24.52
stream22	-3.3229	-52.266	6.3	13.43	1.13	28.56	2.79	3.38
stream23	-3.5441	-51.617	19.97	9.36	0.52	17.13	1.18	3.33
stream24	-3.4982	-51.678	97.41	4.32	1.56	90.04	1.6	3.79
stream25	-3.6409	-51.55	86.84	5	1.95	7.35	0.14	2.57
stream26	-3.6719	-51.487	100	4.46	2.95	373.93	2.24	8.84
stream27	-3.0835	-51.767	68.41	13.25	1.97	9.5	3.56	3.56
stream28	-3.491	-51.583	60.53	9.87	1.82	525.61	5.45	15.02
stream29	-3.6606	-51.514	100	6.18	7.85	36.07	0.13	4.79
stream30	-3.6794	-52.511	48.24	14.4	1.43	12.62	2.99	3.65

Table S5 List of fish species sampled in 30 streams in the region of Volta Grande do Xingu, state of Pará, Brazilian Eastern Amazon. Occurrence refers to the total number of streams where the species were found. Total abundance of species captured in the two sampling events.

Order	Occurrence	Abundance
Family		
Species		
CHARACIFORMES		
ANOSTOMIDAE		
<i>Leporinus cf. granti</i> Eigenmann, 1912	2	2
<i>Leporinus friderici</i> (Bloch, 1794)	5	13
<i>Leporinus torrenticola</i> Birindelli, Teixeira & Britski 2016	2	2
BRYCONIDAE		
<i>Brycon falcatus</i> Müller & Troschel, 1844	2	4
CHARACIDAE		
<i>Astyanax anterior</i> Eigenmann 1908	2	3
<i>Astyanax gr. bimaculatus</i> (Linnaeus, 1758)	22	311
<i>Creagrutus cf. ignotus</i> Vari & Harold 2001	2	6
<i>Ctenobrycon spilurus</i> (Valenciennes, 1850)	1	3
<i>Hemigrammus bellottii</i> (Steindachner, 1882)	1	8
<i>Hemigrammus ocellifer</i> (Steindachner, 1882)	1	6
<i>Hemigrammus</i> sp. “collettii”	11	437
<i>Hyphessobrycon copelandi</i> Durbin, 1908	3	23
<i>Hyphessobrycon heterorhabdus</i> (Ulrey, 1894)	2	37
<i>Hyphessobrycon juruna</i> Faria, Lima & Bastos 2018	3	276
<i>Hyphessobrycon</i> sp. “faixa negra”	2	2
<i>Jupiaba polylepis</i> (Günther, 1864)	5	132
<i>Knodus aff. savannensis</i>	17	1942
<i>Moenkhausia celibela</i> Marinho & Langeani, 2010	4	290
<i>Moenkhausia comma</i> Eigenmann, 1908	7	116
<i>Moenkhausia oligolepis</i> (Günther, 1864)	22	594
<i>Moenkhausia pirauba</i> Zanata, Birindelli & Moreira, 2010	6	21
<i>Moenkhausia xinguensis</i> (Steindachner, 1882)	1	1
<i>Phenacogaster aff. calverti</i> (Fowler 1941)	1	63
<i>Phenacogaster aff. napoatilis</i> Lucena & Malabarba 2010	7	279
<i>Poptella aff. compressa</i> (Günther 1864)	1	4
<i>Poptella brevispina</i> Reis, 1989	5	62
<i>Serrapinnus tocantinensis</i> Malabarba & Jerep 2014	2	57
<i>Tetragonopterus argenteus</i> Cuvier, 1816	1	1
<i>Tetragonopterus chalceus</i> Spix & Agassiz, 1829	1	1
CRENUCHIDAE		
<i>Characidium aff. zebra</i> Eigenmann, 1909	9	141
<i>Microcharacidium aff. weitzmani</i> Backup, 1993	2	67
CURIMATIDAE		
<i>Cyphocharax gouldingi</i> Vari, 1992	3	18

ERYTHRINIDAE

<i>Erythrinus erythrinus</i> (Bloch & Schneider, 1801)	12	112
<i>Hoplerythrinus unitaeniatus</i> (Spix & Agassiz, 1829)	6	64
<i>Hoplias curupira</i> Oyakawa & Mattox, 2009	1	1
<i>Hoplias malabaricus</i> (Bloch, 1794)	22	82

HEMIODONTIDAE

<i>Bivibranchia velox</i> (Eigenmann & Myers, 1927)	1	1
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IGUANODECTIDAE

<i>Bryconops</i> aff. <i>caudomaculatus</i> (Günther, 1864)	1	5
<i>Bryconops</i> aff. <i>magoi</i> Chernoff & Machado-Allison, 2005	1	2
<i>Bryconops affinis</i> (Günther, 1864)	6	113
<i>Bryconops melanurus</i> (Bloch, 1794)	2	15
<i>Iguanodectes rachovii</i> Regan, 1912	2	12

LEBIASINIDAE

<i>Copella arnoldi</i> (Regan, 1912)	7	1062
<i>Pyrrhulina</i> sp. N	4	19

PROCHILODONTIDAE

<i>Prochilodus nigricans</i> Spix & Agassiz, 1829	1	1
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SERRASALMIDAE

<i>Myloplus rubripinnis</i> (Müller & Troschel, 1844)	1	3
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CYPRINODONTIFORMES**CYNOLEBIIDAE**

<i>Anablepsoides xinguensis</i> (Costa, 2010)	14	77
<i>Melanorivulus rubroreticulatus</i> Costa, Amorim & Bragança, 2014	1	1

POECILIIDAE

<i>Pamphorichthys araguaiensis</i> Costa 1991	1	3
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GYMNOTIFORMES**GYMNOTIDAE**

<i>Gymnotus carapo</i> Linnaeus, 1758	13	125
<i>Gymnotus coropinae</i> Hoedeman, 1962	2	3

HYPOPOMIDAE

<i>Brachyhypopomus</i> aff. <i>regani</i> Crampton, de Santana, Waddell & Lovejoy 2017	3	7
<i>Brachyhypopomus beebei</i> (Schultz, 1944)	11	51
<i>Microsternarchus</i> aff. <i>bilineatus</i> Fernández-Yépez, 1968	2	18

RHAMPHICHTHYIDAE

<i>Gymnorhamphichthys rondoni</i> (Miranda Ribeiro, 1920)	8	60
<i>Steatogenys duidae</i> (La Monte, 1929)	1	2

STERNOPYGIDAE

<i>Eigenmannia</i> aff. <i>trilineata</i> López & Castello, 1966	9	42
<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	2	10

MYLIOBATIFORMES**POTAMOTRYGONIDAE**

<i>Potamotrygon</i> aff. <i>orbignyi</i> (Castelnau, 1855)	1	1
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PERCIFORMES

CICHLIDAE		
<i>Aequidens tetramerus</i> (Heckel, 1840)	21	260
<i>Apistogramma geophya</i> Kullander, 1980	2	5
<i>Apistogramma</i> sp.	8	167
<i>Apistogramma</i> sp. tracejado	4	72
<i>Apistogramma</i> sp. vielfleck	1	2
<i>Crenicichla</i> gr. <i>saxatilis</i> (Linnaeus, 1758)	15	108
<i>Satanoperca</i> aff. <i>jurupari</i> (Heckel, 1840)	2	28
SILURIFORMES		
AUCHENIPTERIDAE		
<i>Auchenipterichthys punctatus</i> (Valenciennes, 1840)	1	1
<i>Tatia</i> aff. <i>gyrina</i> (Eigenmann & Allen, 1942)	1	5
<i>Tatia intermedia</i> (Steindachner, 1877)	2	3
<i>Trachelyopterus porosus</i> Eigenmann & Eigenmann, 1888	1	1
CALLICHTHYIDAE		
<i>Callichthys callichthys</i> (Linnaeus, 1758)	9	36
<i>Corydoras</i> cf. <i>aeneus</i> (Gill, 1858)	11	78
<i>Megalechis picta</i> (Müller & Troschel, 1849)	9	18
CETOPSIDAE		
<i>Cetopsidium orientale</i> (Vari, Ferraris & Keith 2003)	1	4
<i>Denticetopsis epa</i> Vari, Ferraris & de Pinna 2005	2	4
<i>Helogenes marmoratus</i> Günther, 1863	2	23
HEPTAPTERIDAE		
<i>Imparfinis</i> aff. <i>hasemani</i> Steindachner, 1917	3	10
<i>Phenacorhamdia</i> sp.	3	5
<i>Pimelodella</i> sp. “faixa grossa”	12	30
<i>Rhamdia quelen</i> (Quoy & Gaimard 1824)	12	50
LORICARIIDAE		
<i>Ancistrus</i> sp. “bola”	8	40
<i>Curculionichthys</i> sp. “alto”	2	6
<i>Hypostomus</i> aff. <i>plecostomus</i> (Linnaeus, 1758)	6	11
<i>Hypostomus hemicochliodon</i> Kner, 1854	2	3
<i>Otocinclus</i> cf. <i>hasemani</i> Steindachner 1915	6	50
<i>Rineloricaria lanceolata</i> (Günther, 1868)	7	15
<i>Rineloricaria</i> sp.	5	12
TRICHOMYCTERIDAE		
<i>Ituglanis</i> aff. <i>amazonicus</i> (Steindachner 1882)	7	64
SYNBRANCHIFORMES		
SYNBRANCHIDAE		
<i>Synbranchus</i> aff. <i>madeira</i> Rosen & Rumney, 1972	14	29
Total	30	7954

Table S6. List of fish species included in the joint species distribution model. The predicted Pseudo R² and RMSE using 2-fold cross-validation. * = predicted R² value not calculated

Species	Explanatory power		Predictive power	
	Pseudo R ²	RMSE	Pseudo R ²	RMSE
<i>Aequidens tetramerus</i>	0.65	2.55	0.17	10.40
<i>Anablepsoides xinguensis</i>	0.43	1.15	-	5.84
<i>Ancistrus</i> sp. "bola"	0.35	1.21	0.05	3.46
<i>Apistogramma</i> sp.	0.41	2.15	0.09	21.68
<i>Apistogramma</i> sp. "tracejado"	0.21	1.50	0.02	19.04
<i>Astyanax</i> aff. <i>bimaculatus</i>	0.55	6.11	0.08	20.95
<i>Brachyhypopomus</i> aff. <i>regani</i>	0.14	0.26	0.52	1.59
<i>Brachyhypopomus beebei</i>	0.47	1.29	0.14	2.93
<i>Bryconops affinis</i>	0.39	2.30	0.15	8.59
<i>Callichthys callichthys</i>	0.24	0.90	0.02	3.84
<i>Characidium</i> aff. <i>zebra</i>	0.42	5.09	0.09	18.06
<i>Copella arnoldi</i>	0.43	15.41	0.12	132.15
<i>Corydoras</i> cf. <i>aeneus</i>	0.37	1.41	0.04	5.62
<i>Crenicichla</i> gr. <i>saxatilis</i>	0.50	2.78	-	9.11
<i>Cyphocharax gouldingi</i>	0.18	0.46	-	2.68
<i>Eigenmannia</i> aff. <i>trilineata</i>	0.18	1.60	0.01	4.60
<i>Erythrinus erythrinus</i>	0.53	1.69	0.11	7.60
<i>Gymnorhamphichthys rondoni</i>	0.36	1.81	-	4.62
<i>Gymnotus carapo</i>	0.35	2.37	0.19	6.76
<i>Hemigrammus</i> sp. "collettii"	0.61	6.80	0.21	22.79
<i>Hoplerethrinus unitaeniatus</i>	0.26	0.84	0.09	9.41
<i>Hoplias malabaricus</i>	0.52	1.26	-	2.74
<i>Hyphessobrycon copelandi</i>	0.11	1.43	-	7.46

<i>Hyphessobrycon juruna</i>	0.19	2.10	0.33	60.26
<i>Hypostomus</i> aff. <i>plecostomus</i>	0.29	0.43	0.07	0.90
<i>Imparfinis</i> aff. <i>hasemani</i>	0.15	0.38	-	1.80
<i>Ituglanis</i> aff. <i>amazonicus</i>	0.34	0.80	0.14	8.47
<i>Jupiaba polylepis</i>	0.28	1.23	0.31	10.90
<i>Knodus</i> aff. <i>savannensis</i>	0.89	18.53	0.49	57.78
<i>Leporinus friderici</i>	0.21	0.56	0.17	1.57
<i>Megalechis picta</i>	0.21	0.63	0.10	1.36
<i>Moenkhausia celibela</i>	0.18	2.70	0.25	57.67
<i>Moenkhausia comma</i>	0.39	2.29	0.09	6.96
<i>Moenkhausia oligolepis</i>	0.64	9.83	0.09	30.59
<i>Moenkhausia pirauba</i>	0.19	0.98	0.01	3.88
<i>Otocinclus</i> cf. <i>hasemani</i>	0.26	0.62	0.01	6.54
<i>Phenacogaster</i> aff. <i>napoatilis</i>	0.42	1.93	0.22	51.17
<i>Phenacorhamdia</i> sp.	0.09	0.32	0.00	1.14
<i>Pimelodella</i> sp. "faixa grossa"	0.36	0.69	0.03	1.61
<i>Poptella brevispina</i>	0.24	1.50	0.07	12.28
<i>Pyrrhulina capim</i>	0.27	0.52	0.10	1.93
<i>Rhamdia quelen</i>	0.42	0.78	0.22	4.03
<i>Rineloricaria lanceolata</i>	0.20	0.51	0.02	1.25
<i>Rineloricaria</i> sp.	0.21	0.49	0.09	1.24
<i>Synbranchus</i> aff. <i>madeira</i>	0.36	0.58	0.06	1.27

Table S7 Variance partitioning results per variable and per species. A red colour indicates the variable that explained more of that species abundance.

Species	PC1	PC2	PC3	Forest cover	Catchment slope	Catchment area	Drainage network extension	Distance to large river	Random: Stream	Random: Spatial autocorrelation
<i>Aequidens tetramerus</i>	0.11	0.02	0.03	0.03	0.03	0.15	0.03	0.05	0.26	0.29
<i>Anablepsoides xinguensis</i>	0.37	0.03	0.09	0.08	0.05	0.07	0.05	0.02	0.22	0.02
<i>Ancistrus</i> sp. "bola"	0.02	0.16	0.04	0.03	0.17	0.03	0.04	0.02	0.46	0.02
<i>Apistogramma</i> sp.	0.07	0.19	0.01	0.03	0.25	0.01	0.05	0.02	0.02	0.36
<i>Apistogramma</i> sp. "tracejado"	0.04	0.08	0.08	0.06	0.28	0.01	0.26	0.08	0.02	0.1
<i>Astyanax</i> aff. <i>bimaculatus</i>	0.03	0.09	0.04	0.11	0.11	0.03	0.02	0.05	0.06	0.45
<i>Brachyhypopomus</i> aff. <i>regani</i>	0.23	0.24	0.03	0.16	0.19	0.02	0.04	0.05	0.01	0.03
<i>Brachyhypopomus beebei</i>	0.14	0.07	0.05	0.04	0.14	0.09	0.13	0.11	0.01	0.22
<i>Bryconops affinis</i>	0.03	0.03	0.02	0.19	0.16	0.09	0.12	0.06	0.23	0.06
<i>Callichthys callichthys</i>	0.46	0.08	0.03	0.03	0.03	0.1	0.04	0.12	0.07	0.04
<i>Characidium</i> aff. <i>zebra</i>	0	0.01	0.12	0.02	0.23	0.03	0.16	0.07	0.25	0.11
<i>Copella arnoldi</i>	0.06	0.17	0.02	0.05	0.18	0.01	0.02	0.02	0.44	0.03
<i>Corydoras</i> cf. <i>aeneus</i>	0.02	0.02	0.09	0.28	0.09	0.05	0.09	0.04	0.17	0.15
<i>Crenicichla</i> gr. <i>saxatilis</i>	0.03	0.07	0.06	0.08	0.03	0.01	0.04	0.03	0.65	0.02

<i>Cyphocharax gouldingi</i>	0.01	0.04	0.05	0.05	0.39	0.01	0.37	0.05	0.03	0.01
<i>Eigenmannia</i> aff. <i>trilineata</i>	0.04	0.02	0.14	0.07	0.04	0.02	0.28	0.1	0.26	0.03
<i>Erythrinus erythrinus</i>	0.09	0.34	0.01	0.03	0.23	0.08	0.03	0.02	0.13	0.05
<i>Gymnorhamphichthys rondoni</i>	0.01	0.22	0.02	0.16	0.15	0.04	0.04	0.24	0.03	0.09
<i>Gymnotus carapo</i>	0.21	0.06	0.12	0.07	0.19	0.07	0.02	0.03	0.1	0.13
<i>Hemigrammus</i> sp. "collettii"	0	0.03	0.13	0.16	0.09	0.01	0.07	0.07	0.03	0.4
<i>Hoplerethrinus unitaeniatus</i>	0.13	0.14	0.01	0.03	0.14	0.03	0.09	0.2	0.16	0.06
<i>Hoplias malabaricus</i>	0.32	0.02	0.2	0.1	0.07	0.02	0.06	0.03	0.08	0.1
<i>Hyphessobrycon copelandi</i>	0.01	0.14	0.05	0.03	0.06	0.03	0.06	0.08	0.02	0.51
<i>Hyphessobrycon juruna</i>	0.02	0.04	0.24	0.03	0.1	0.03	0.11	0.05	0.01	0.36
<i>Hypostomus</i> aff. <i>plecostomus</i>	0.03	0.12	0.08	0.14	0.15	0.02	0.32	0.07	0.01	0.06
<i>Imparfinis</i> aff. <i>hasemani</i>	0.24	0.21	0.02	0.11	0.17	0.04	0.13	0.06	0.01	0
<i>Ituglanis</i> aff. <i>amazonicus</i>	0.17	0.27	0.01	0.08	0.2	0.02	0.02	0.03	0.08	0.11
<i>Jupiaba polylepis</i>	0.07	0.01	0.24	0.02	0.21	0	0.3	0.14	0	0
<i>Knodus</i> aff. <i>savannensis</i>	0	0.01	0	0.02	0.29	0.01	0.2	0.05	0.37	0.05
<i>Leporinus friderici</i>	0.16	0.04	0.15	0.04	0.14	0.01	0.32	0.13	0.01	0.01
<i>Megalechis picta</i>	0.26	0.04	0.06	0.05	0.16	0.1	0.05	0.18	0.06	0.03
<i>Moenkhausia celibela</i>	0	0.1	0.05	0.09	0.1	0.01	0.11	0.12	0.01	0.4

<i>Moenkhausia comma</i>	0.01	0.02	0.1	0.04	0.06	0.01	0.05	0.09	0.56	0.06
<i>Moenkhausia oligolepis</i>	0.02	0.09	0	0.11	0.08	0.03	0.12	0.01	0.04	0.5
<i>Moenkhausia pirauba</i>	0.06	0.03	0.03	0.05	0.23	0.02	0.28	0.24	0.04	0.02
<i>Otocinclus</i> cf. <i>hasemani</i>	0.19	0.14	0.09	0.31	0.06	0.04	0.06	0.08	0.01	0.02
<i>Phenacogaster</i> aff. <i>napoatilis</i>	0.03	0.06	0.01	0.02	0.23	0.07	0.21	0.02	0.02	0.33
<i>Phenacorhamdia</i> sp.	0.07	0.06	0.06	0.07	0.25	0.02	0.36	0.08	0.02	0.01
<i>Pimelodella</i> sp. "faixa grossa"	0.03	0.04	0.02	0.39	0.17	0.01	0.17	0.16	0	0.01
<i>Poptella brevispina</i>	0.14	0.1	0.03	0.16	0.04	0.04	0.13	0.21	0.12	0.03
<i>Pyrhulina capim</i>	0.06	0.08	0.03	0.05	0.05	0.03	0.08	0.04	0.36	0.23
<i>Rhamdia quelen</i>	0.01	0.1	0.07	0.19	0.03	0.05	0.03	0.14	0.25	0.14
<i>Rineloricaria lanceolata</i>	0.05	0.06	0.38	0.08	0.1	0.08	0.14	0.04	0.02	0.05
<i>Rineloricaria</i> sp.	0.04	0.06	0.04	0.19	0.1	0.05	0.27	0.13	0.07	0.04
<i>Synbranchus</i> aff. <i>madeira</i>	0.41	0.11	0.09	0.05	0.15	0.03	0.04	0.09	0.03	0.01
Mean variance explained across all species	0.1	0.09	0.07	0.09	0.14	0.04	0.12	0.08	0.13	0.13

Figures

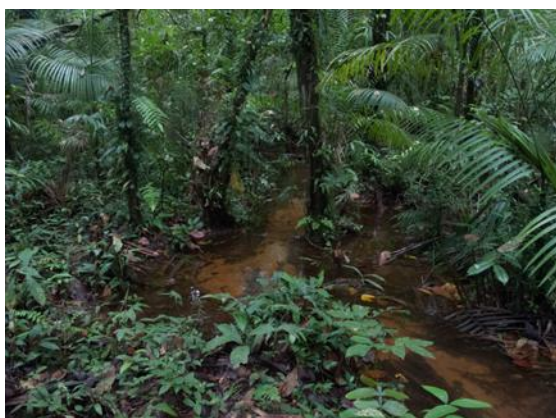


Figure S1 Examples of streams sampled in the region of Volta Grande do Xingu, state of Pará, Brazilian eastern Amazon.

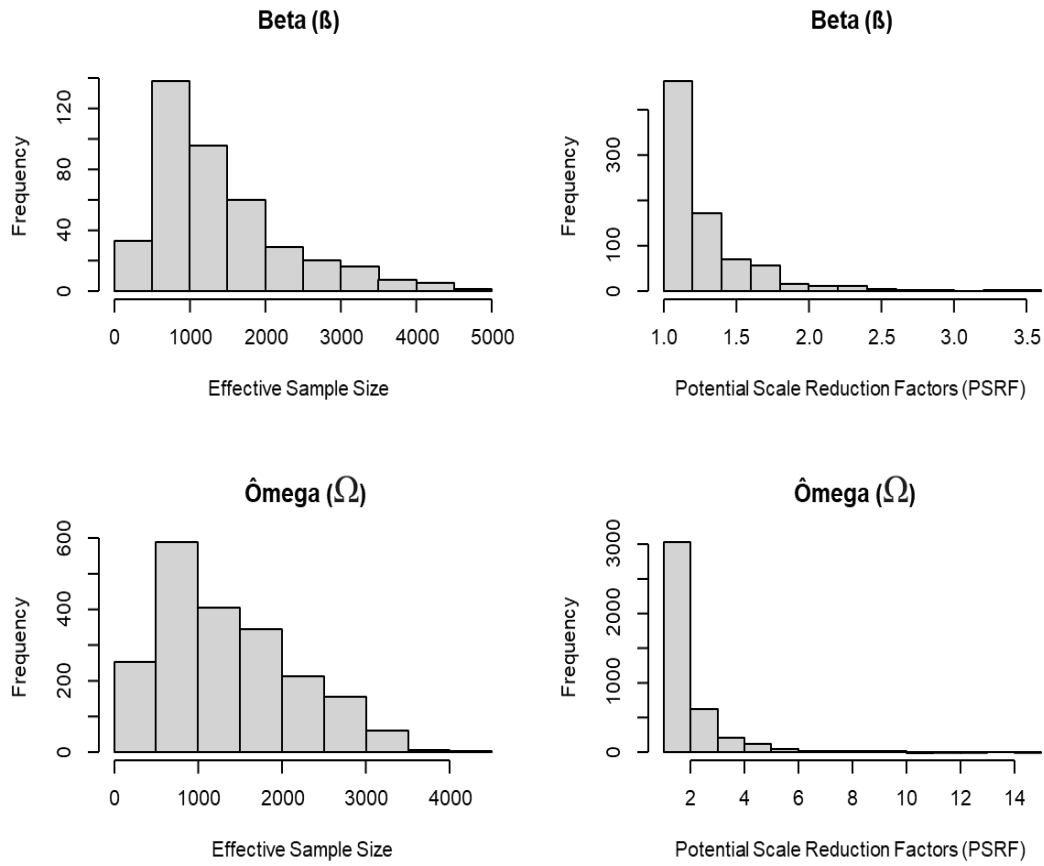


Figure S2 Histograms of effective sample sizes and potential downscaling factors (PSRF) for beta (β - variable species ratio) and omega (Ω - co-occurrence) parameters of hierarchical modeling of fish species.

Supplementary S2

Local environmental variables were subjected to principal component analysis (PCA) to reduce data dimensionality and create orthogonal axes. We first conducted a principal component analysis (PCA) to identify which substrate variables (clay, sand, trunk, litter, fine litter, root, macrophytes, rocks and pebble/gravel) most contribute to characterizing stream substrates) (Supplementary S2: Table S8 and Figure S3).

Table S8 Loadings of substrate proportions in the PC axes of the substrate composition of 30 stream plots in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon. Bold values indicate the variables with higher weights in axis 1 and 2, which were selected to characterize the stream substrates.

Substrate Composition	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Sand	-0.547	-0.198	0.240	-0.239	0.255	-0.100	-0.342	-0.172	0.570
Clay	-0.256	0.286	0.176	-0.093	-0.805	0.190	0.242	-0.061	0.260
Pebble/gravel	0.302	-0.214	0.192	0.697	-0.274	-0.193	-0.364	-0.200	0.237
Fine litter	0.615	0.082	0.051	-0.343	0.023	-0.178	0.083	0.361	0.570
Aquatic plants	0.333	-0.405	0.200	-0.204	0.054	0.628	0.137	-0.475	0.033
Coarse litter	0.165	0.629	0.048	-0.059	0.202	-0.259	0.052	-0.678	0.024
Roots	-0.102	0.317	0.395	0.470	0.404	0.372	0.318	0.265	0.198
Rock	-0.119	-0.205	-0.655	0.252	0.071	-0.060	0.499	-0.192	0.396
Trunk	0.051	0.352	-0.495	0.038	0.003	0.530	-0.559	0.063	0.170
Proportion explained (%)	22.99	20.94	17.31	11.19	10.13	8.32	5.83	2.45	1.00

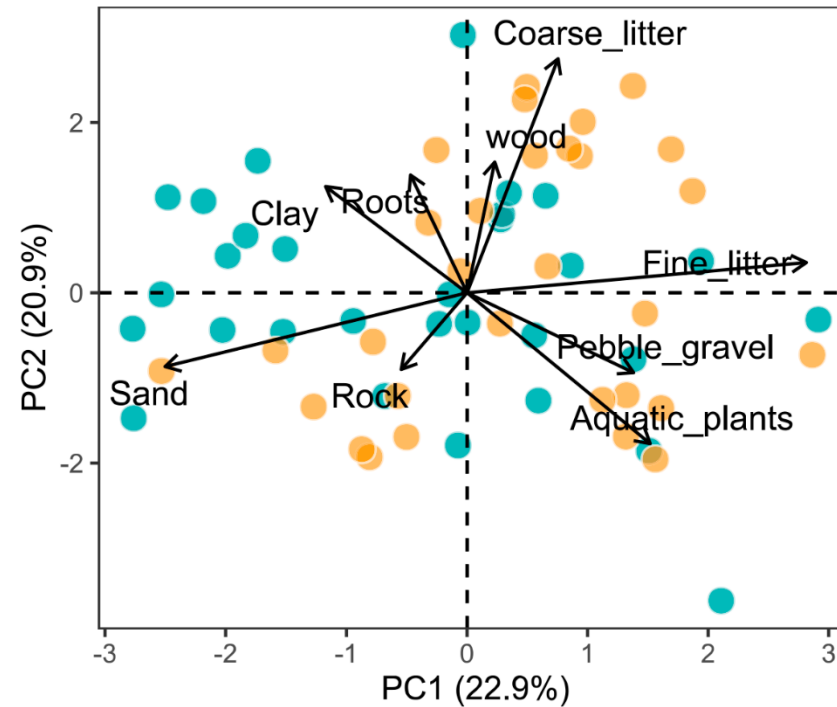


Figure S3. Principal component analysis (PCA) for substrate composition of 30 stream plots in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon. Dry season sampling (orange circles) and rainy season sampling (cyan circles).

Then we performed principal component analysis (PCA) using the main substrate variables (sand, coarse litter, fine litter, macrophytes), physicochemical variables (conductivity, pH, dissolved oxygen, saturated oxygen and temperature) and local structural variables (Channel depth (m), Channel width (m), and canopy cover (%)). As the predictors had different scales and variances, the second PCA was performed from the standardized and centralized data so that the variables contributed equally to the ordering (Supplementary S2: Table S9 and Figure S4).

Table S9 Loadings of the local environmental variables in the PC axes of the environmental variables of 30 stream plots in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon. Bold values indicate the variables with higher weights in axis 1, 2 and 3, which were selected to characterize the local environmental conditions of the streams.

Substrate Composition	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
pH	-0.25	-0.08	-0.16	-0.21	-0.89	-0.05	0.11	-0.21	0.00	-0.06	0.09
Temperature	0.11	0.42	-0.06	0.58	-0.12	-0.07	0.50	0.06	-0.41	-0.10	0.14
Conductivity	0.37	-0.10	-0.33	-0.32	-0.07	0.43	0.29	0.53	0.03	-0.28	-0.02
Dissolved oxygen	0.42	-0.04	-0.15	-0.45	0.13	-0.37	-0.03	-0.34	-0.56	-0.11	0.07
Sand	0.34	0.06	0.48	-0.09	-0.28	-0.31	-0.14	0.50	0.00	0.35	0.27
Fine litter	-0.41	0.01	-0.42	-0.15	0.25	-0.31	0.12	0.24	0.09	0.10	0.62
Aquatic plants	-0.09	0.52	-0.30	-0.24	-0.01	-0.16	0.06	0.14	0.02	0.46	-0.56
Coarse litter	-0.20	-0.43	-0.26	0.30	-0.09	-0.12	-0.38	0.39	-0.48	0.01	-0.27
Channel depth	0.39	-0.04	-0.44	0.25	-0.09	0.32	-0.27	-0.25	0.08	0.51	0.28
Channel width	0.33	-0.30	-0.23	0.26	-0.04	-0.57	0.21	-0.03	0.50	-0.12	-0.22
Canopy cover	-0.10	-0.51	0.18	-0.07	0.10	0.10	0.60	-0.08	-0.17	0.52	-0.09
Proportion explained (%)	26.16	21.88	13.34	8.39	7.97	5.46	5.06	4.47	3.32	2.19	1.76

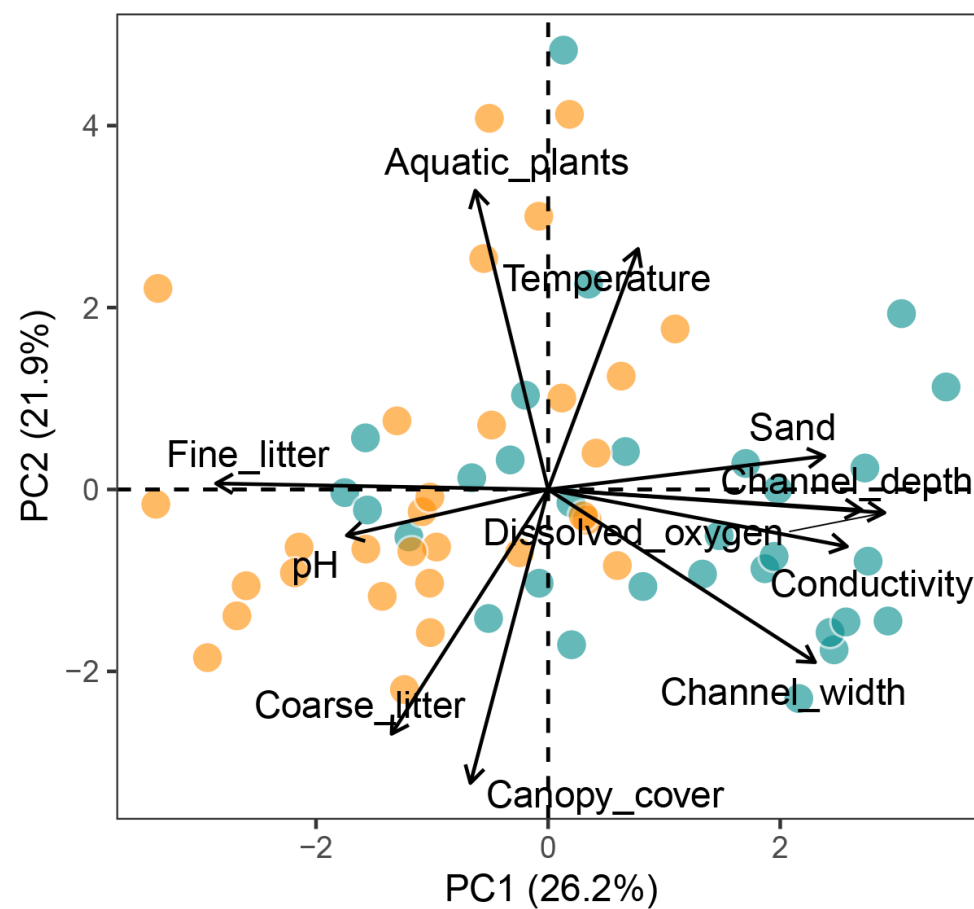
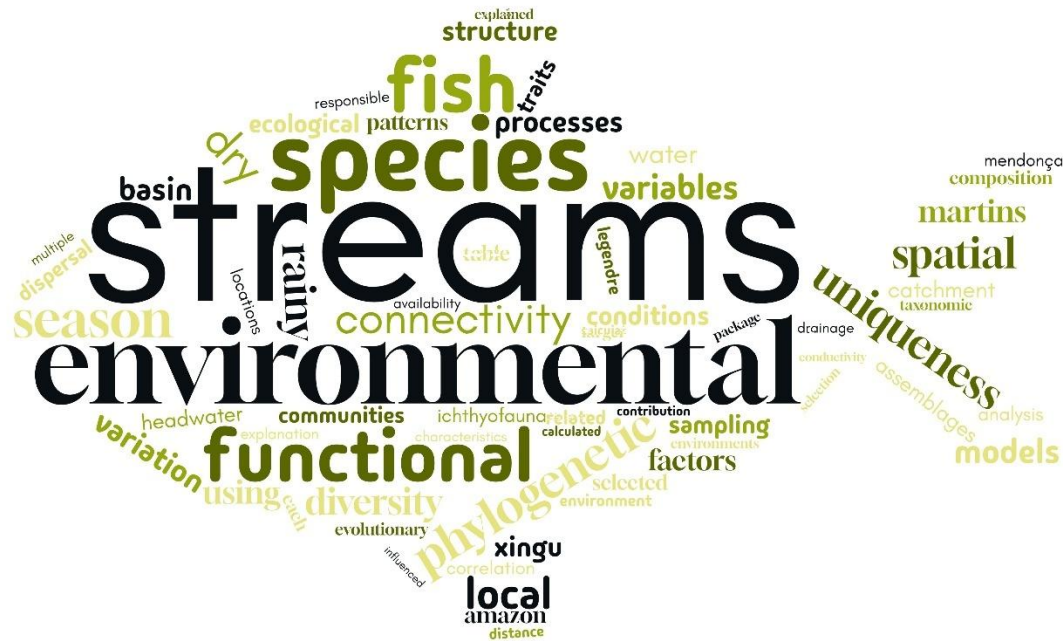


Figure S4. Principal component analysis (PCA) for the local environmental variables of 30 stream plots in the region of Volta Grande do Xingu, state of Pará, Eastern Brazilian Amazon. Dry season sampling (orange circles) and rainy season sampling (cyan circles).



The role of the environment and connectivity on multiple facets of local fish diversity in tropical headwater streams

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The role of the environment and connectivity on multiple facets of local fish diversity in tropical headwater streams

Abstract

1. The identification of multiple facets of biodiversity (e.g., phylogenetic, and functional) can help to understand how evolutionary and ecological mechanisms shape the assembly of biological communities.

2. Here, we employed multiple regressions and variance partitions to investigate the effects of environmental conditions, connectivity, and space on aspects of the functional and phylogenetic facets of fish fauna in tropical headwater streams of the Xingu River basin, in Eastern Amazonia.

3. We found that the functional and phylogenetic diversities of fish communities are related to local environmental conditions and stream connectivity in the drainage network, with marked differences occurring between the rainy and dry periods. Furthermore, we discovered that functional uniqueness was influenced mainly by environmental factors, while phylogenetic uniqueness had a more complex relationship with the influence of local environmental factors and connectivity.

4. Our findings indicate that the fish assemblages of small headwater streams of the Xingu River basin share a close phylogenetic history. This is probably because of the climatic and environmental stability experienced by Amazonian ichthyofauna over evolutionary time.

5. Our findings emphasize the role of niche-based processes in shaping the unique functional composition of fish assemblages in headwater streams, and highlight the importance of environmental heterogeneity in maintaining the ecological integrity of these freshwater ecosystems.

Keywords: Functional diversity, Phylogenetic diversity, Ecological uniqueness, Spatial variation, Amazon ichthyofauna

Introduction

The biodiversity patterns of biological communities are determined by a combination of many factors which occur at multiple spatial and temporal scales (Vellend, 2016). At local scales, the environment is a key factor in structuring composition and diversity (Poff, 1997). However, species coexistence patterns at local scales are strongly influenced by the phylogenetic structure of communities (Villalobos et al., 2013) and by the diversity of functional traits within the regional species pool (Mohammed et al., 2022). These traits are closely linked to the evolutionary and ecological history of a given region (Castillo-Escrivà et al., 2017; Rodrigues-Filho et al., 2018a). Such legacies determine the composition and diversity of biological communities due to the direct effect of contemporary processes related to dispersal capacity and niche-based processes (Vellend, 2016), and can vary depending on the spatial configuration and the taxonomic group analyzed (Heino, 2013a; Schmera et al., 2018; Tonkin et al., 2018).

The organization of the composition and diversity of fish assemblages in Neotropical streams has been attributed to historical (e.g., speciation and extinction events) and biogeographical (e.g., geographical barriers and dispersion) factors, which are responsible for the composition of the available regional species pool (Dagosta & Pinna, 2019; Rodrigues-Filho et al., 2018). Thereafter, the environmental conditions that structure a fish assembly in streams can be correlated with the limnological and structural characteristics of these environments, such as pH, water conductivity, stream size, depth, width of channel, and substrate type (Fernandes et al., 2013; Leal et al., 2016; Martins et al., 2024; Mendonça et al., 2005). However, these variables are influenced by variables at the basin scale (e.g. geology, climate and the vegetation structure of the river basin) (Benone et al., 2017; Frissell et al., 1986; Leal et al., 2016). Thus, the contribution of environmental processes (i.e., niche-based) in structuring fish assemblages operate at different spatial scales (Benone et al., 2020; Hoeinghaus et al., 2007; Macedo et al., 2014; Paller et al., 2016).

The ichthyofauna of small *terra-firme* streams in the Amazon comprise a large concentration of species with restricted distributions and limited ability to migrate (Castro, 1999; Mendonça et al., 2005). As a result, the configuration and position of streams in drainage networks can be fundamental to the dynamics of fish assemblages. The dendritic characteristic of drainage networks limits the dynamics of local dispersion and colonization (Brown et al., 2011; Fagan, 2002). Structural variables such as width, depth, current velocity, substrate, and canopy cover in small streams differ from those in larger water bodies. For

instance, small streams have a higher availability of submerged branches and trunks, providing a complex structure that can serve as a habitat for various species. However, as we move to larger streams, light availability increases due to reduced canopy cover. This increased exposure to sunlight can result in higher water temperatures in larger streams compared to smaller ones (Fernandes et al., 2013; Vannote et al., 1980). With this, the position of the stream in relation to large rivers can facilitate the recruitment of populations that inhabit these systems. Thus, streams with similar structural characteristics may present distinct fish assemblages according to their position within the drainage network (Stegmann et al., 2019).

Despite the recognized importance of historical processes in the organization of fish assemblages in Neotropical streams (Rodrigues-Filho et al., 2018), studies that measure the direct effect of these processes are rare (Aquino & Colli, 2017; Roa-Fuentes et al., 2019, 2022; Rodrigues-Filho et al., 2018). In this context, phylogenetic diversity (PD), a metric that considers the evolutionary relationship of species in a local community (Jones et al., 2019; Scheiner et al., 2017), and functional diversity (FD), which measures the variability of specific traits among species in a community (Tilman, 2001), can be used to provide important information on how abiotic filters select organisms with suitable characteristics to survive in an environment (Cardoso et al., 2014; Jones et al., 2019).

Over the past few decades, in addition to indices that measure local diversity using functional and phylogenetic characteristics (i.e., alpha diversity), techniques that capture changes in community structures (i.e., beta diversity) have also been expanded to address functional and phylogenetic data (e.g., Villéger et al. 2011, Shooner et al. 2018, Heino et al. 2022). Within this expansion, ecological uniqueness (i.e., the local contribution to beta diversity - LCBd; Legendre and De Cáceres 2013) was initially proposed for addressing taxonomic data (e.g., Vilmi et al. 2017, Schneck et al. 2022), and has been applied to functional information (e.g., Heino et al. 2022) and phylogenetic information (e.g., Shooner et al. 2018). High LCBd values may correspond to areas with unique ecological conditions (Legendre & De Cáceres, 2013). High functional LCBd values can indicate locations with the presence of exclusive traits or with a low number of traits in local communities (Heino et al. 2022), and thus the potential for functional uniqueness to determine the role of environmental filtering in the selection of traits present in local communities (Quirino et al., 2021). From a phylogenetic perspective, phylogenetically unique locations may indicate the influence of historical factors on the distribution pattern of species in current communities (e.g., Shooner et al. 2018).

The Amazon Basin has the most diverse freshwater ichthyofauna on Earth, both in terms of taxonomic diversity (Dagosta & Pinna, 2019) and functional diversity (Toussaint et al., 2016). This high biological diversification is partly explained by the climatic and environmental stability experienced by these communities over evolutionary time (Oberdorff et al., 2019; Peres et al., 2010). Recent results also show nonrandom patterns in phylogenetic diversity of the Amazon ichthyofauna, indicating a deeper evolutionary divergence between taxa in the eastern subbasins and more recent radiations in the western subbasins (Salgueiro et al., 2022). In the Xingu region (Western Amazon), for example, the genetic structure and demographic history of a Loricariidae species (*Baryancistrus xanthellus*) were shaped by historical climate changes (Magalhães et al., 2021). The increase in precipitation (approximately 200,000 years ago) may have influenced the expansion of rocky environments (habitats of *B. xanthellus*) in tributaries of the Xingu River and the reduction of these habitats in the main channel of the Xingu River.

Identifying multiple facets of biodiversity (i.e. taxonomic, phylogenetic, and functional) can help to understand how evolutionary and ecological mechanisms shape the assembly of biological communities (Girardello et al. 2019). Earlier, from the classical approach (taxonomic facet), dispersal limitation together with environmental conditions (at multiple scales) and the configuration of the drainage network were shown to be key factors in the organization of fish assemblages in the *terra-firme* streams of the Xingu basin (eastern Amazon) (Martins et al., 2024). We evaluated the contributions of environmental conditions, the connectivity of water bodies in the drainage network and spatial factors to the functional and phylogenetic structure of the ichthyofauna of these small streams. Initially, assuming that the functionality of species and evolutionary histories were direct results of processes linked to adaptation to environmental conditions, we predicted that (i) environmental factors were responsible for the variations in functional diversity (FD) and phylogenetic diversity (PD). Furthermore, we postulated that (ii) functional uniqueness is the result of environmental filtering and processes related to dispersal. Thus, we expected that functional uniqueness would be explained by environmental (local environment and landscape), connectivity and spatial variables together. For phylogenetic uniqueness, we hypothesized is that (iii) phylogenetic uniqueness is explained exclusively by spatial factors. We expect this due to the historical processes of species dispersal in the basin and the low connectivity of the streams. Sites that have lost species over time, caused for example by environmental changes, may not have been recolonized due to the low connectivity between these water bodies and the limited dispersal capacity of the stream ichthyofauna.

Materials and Methods

Study area

The study was carried out in the Volta Grande do Xingu region, Brazilian Eastern Amazon (Figure 1). The region is located in a geological transition area, with sediments from the craton and the Amazon sedimentary basin (Sawakuchi et al., 2015). The climate of the region is tropical, and the average annual air temperature ranges from 25 to 27 °C (Estupinan & Camargo, 2009). The annual rainfall reaches 1963 mm, with a well-defined dry season occurring between June and November and a rainy period occurring from December to May (Santos et al., 2016). The investigated streams have slightly acidic waters, with a mean pH of 6.4 and low conductivity, averaging 0.31 mScm^{-1} . They contain well-oxygenated waters with an average oxygen concentration of 6.59 mg L^{-1} and an average temperature of 25.8°C . These streams feature channels with an average width of 2.3 m and a depth of 0.2 m. The stream bottom is predominantly covered by sand, fine litter banks and coarse litter (Martins et al., 2024).

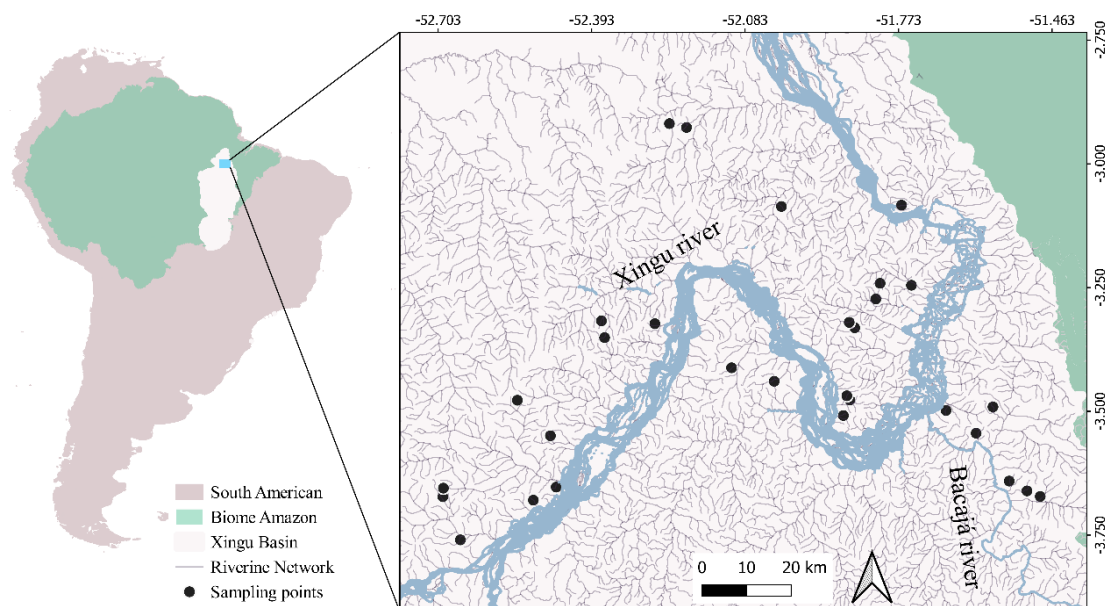


Figure 1 Geographic location of the 30 stream stretches sampled between March 2012 and October 2014 in the region of Volta Grande do Xingu, state of Pará, Brazilian Eastern Amazon.

Sampling design

We sampled 30 headwater streams (first to second order streams, Strahler classification streams) (Figure 1). Field activities took place between March 2012 and October 2014; five sampling events taking place in the rainy season (January-May) and seven in the dry season (July-November) (Table S1). The database has up to 12 sampling events for each stream plot, where the collection of ichthyofauna and environmental characterization were always carried out in the same sections. Some streams completely dried up or were reduced to disconnected pools during the dry season. Furthermore, some streams were not sampled during other collection events because the sites were inaccessible or flooded (Table S1; for more details, see Martins et al. 2022).

All the sampled streams were small, allowing for efficient sampling of ichthyofauna. The size of the sampled stream section (50-meter section) was determined by previous studies and resulted in the collection protocol of the *Igarapés Project* (<https://ppbio.inpa.gov.br/sites/default/files/Peixes.pdf>) (Mendonça et al., 2005). This methodology, which evaluates both the local fish community and environmental characteristics, has been widely applied in Amazonian streams (Borba et al., 2021; Dias et al., 2010; Martins et al., 2022; Mendonça et al., 2005; Rodrigues-Filho et al., 2018; Stegmann et al., 2019).

Local environment and fish sampling

Following the *Igarapés Project* protocol (Mendonça et al., 2005), five equidistant transverse transects distributed along the same 50-m stretch that was used to sample fish species: we recorded the average width (m) and depth (m) of the channel and the average canopy cover (%). We documented the relative composition of the substrate (%) based on the frequency of nine categories: clay, sand, trunk (wood with a diameter larger than 10 cm), litter (comprised of leaves and small branches), fine litter (fine particulate matter), roots (mostly fine roots from marginal vegetation), aquatic plants, rocks and gravel. Water conductivity (mS cm^{-1}), pH, dissolved oxygen (mg L^{-1}) and water temperature ($^{\circ}\text{C}$) were measured with a multiparameter probe (YSI 556).

For the collection of fish, our study employed the methodology established by the *Igarapés Project* (<https://ppbio.inpa.gov.br/sites/default/files/Peixes.pdf>) (Mendonça et al., 2005). This methodology is widely used for assessing both the local fish community and

physical-chemical characteristics in small streams (Borba et al., 2021; Dias et al., 2010; Martins et al., 2022; Mendonça et al., 2005; Oliveira et al., 2020) and has been adopted in approximately 40% of stream fish studies conducted in Brazil up to 2016 (Junqueira et al., 2020). According to the protocol we blocked streams with fine-mesh nets (5 mm between opposite knots). To increase sampling efficacy, a third net was used to subdivide the sampling stretches every 10 meters. Three people explored the reach of the stream, using dip nets, small seine nets, and sieves to capture fish over a 2-hour period or until no fish were observed when moving along the stream reach. After collection, the fish were euthanized with a lethal dose of Eugenol, fixed in a 10% formalin solution, and stored in 70% ethanol for subsequent identification to species level using taxonomic keys (later confirmed by specialists).

Landscape, connectivity, and spatial variables

Landscape variables were catchment area (km²), catchment mean slope (%), and catchment forest cover (%). We calculated the catchment area and mean slope of each watershed using a digital elevation model from the Shuttle Radar Topography Mission (SRTM), obtained from the EarthExplorer website (<http://earthexplorer.usgs.gov/>) and software QGIS (QGIS Development Team 2021). The catchment forest cover (including primary and secondary forests) was determined through the analysis of images from the MapBiomas project (<https://mapbiomas.org/en/colecoes-mapbiomas>) (Souza et al., 2020) using the QGIS software.

To estimate the connectivity of streams, we analyzed four variables: stream link magnitude (Link), downstream link (D-link), extension of the drainage network (EDN), and distance from the mainstream (DMS). To calculate the connectivity variables, we used QGIS software based on the hydrological maps constructed by Venticinque et al., (2016). The selected connectivity variables are related to the possibilities of sampling sites being accessed by new individuals from multiple origins and with distinct processes. The Link (Shreve, 1966) was defined as the number of unbranched source streams upstream from the sampling site. D-Link (Osborne & Wiley, 1992) was defined as the magnitude of the link to the next confluence downstream. Larger confluences are directly connected to a greater availability of individuals from downstream conceptions of the site. The EDN (Martins et al., 2024) represents the availability of environments for ichthyofauna without passing through major environmental filters, such as the main river. The DMS (Martins et al., 2024) is a measure of connectivity between the sample site and potentially similar environments, with greater distances indicating lower connectivity.

Spatial variables were obtained by means of Moran Eigenvector Maps (MEMs; Dray et al., 2006). Fluvial distance provides a better representation of spatial patterns generated by fish dispersal within a dendritic network (Landeiro et al., 2011). Therefore, to represent the spatial structure, the fluvial distance between sampling sites was decomposed into spatial eigenvectors using the *'dbmem'* function of the R package *'adespatial'* (Dray et al., 2023). Only spatially autocorrelated positive eigenvectors were retained for further analysis (Borcard & Legendre, 2002). The fluvial distance between all sites was calculated using the hydrological maps of Venticinque et al., (2016) through the R package *'riverdist'* (Tyers, 2020).

Functional data

Each fish species was characterized by its food acquisition, locomotion, and habitat use (see Leitão et al., 2018 for further details). For this purpose, body mass and morphometric data were collected from adult specimens (one to five per species) and subsequently combined into 12 ecomorphological traits (Table 1 and Table S2). Initially, we defined the number of dimensions that best describes the functional space (Maire et al., 2015). For this, the R package *'mFD'* (Magneville et al., 2022) was used to scale the traits (mean = 0 and standard deviation = 1) and construct a Euclidean distance matrix between each pair of species. Based on this matrix, a Principal Component Analysis (PCA) was used to reduce dimensionality and construct the functional space for all 103 species collected over the three years of sampling. This initial procedure indicated that the first six PCA axes (78.8% of the accumulated variance) were necessary to construct a high-quality functional space that reflects the dissimilarity between species and reduces information loss (Magneville et al., 2022; Maire et al., 2015; Villéger et al., 2008).

Table 2 The 12 ecomorphological traits used to functionally characterize fish species of streams from the region of Volta Grande do Xingu, Pará state, Brazilian Eastern Amazon, and their ecological significance.

Ecomorphological trait	Ecological meaning	Reference
Oral-gape shape	Method to capture food items	Karpouzi & Stergiou, 2003
Oral-gape position	Feeding strategy in the water column	Villéger et al., 2010 adapted from Sibbing & Nagelkerke, 2001
Eye size	Prey detection	Villéger et al., 2010 adapted from Boyle & Horn, 2006
Eye position	Vertical position in the water column	Gatz, 1979
Body transversal shape	Vertical position in the water column and hydrodynamics	Sibbing, Nagelkerke 2001
Body transversal surface	Distribution of mass throughout the body for hydrodynamics	Villéger et al. 2010
Pectoral-fin position	Pectoral-fin use for maneuverability	Dumay et al., 2004
Aspect ratio of the pectoral fin	Pectoral fin propulsion	Villéger et al., 2010 adapted from Fulton et al., 2001
Caudal-peduncle throttling	Swimming efficiency by reducing water resistance	Webb 1984
Aspect ratio of the caudal fin	Propulsion and steering by caudal fin	Webb 1984
Fins surface ratio	Main type of propulsion	Villéger et al. 2010
Mass	Metabolism, endurance, and swimming ability	Villéger et al. 2010

Phylogenetic data

A phylogenetic hypothesis of the study species was developed from the largest and most recent super-tree of actinopterygian fishes (Chang et al., 2019, 2020; Rabosky et al., 2018). In general, the backbone of this global super-tree consists of 11,638 species with genetic data (based on a 27-gene multi-locus alignment), and 19,888 species inserted based on the monophyly of their most restrictive taxonomic classification (e.g., order, family, genus). The super-tree was also calibrated in time with 130 nodes restricted to fossils. The species that were present in the database but not included in the super-tree were carefully added to their corresponding genera, allowing these genera to form polytomies. The addition

of species missing from the phylogeny was performed using the '*congeneric.merge*' function of the R package *pez* (Pearse et al., 2015).

Data analyses

The analyses were carried out for the rainy and dry seasons separately. Initially, for each stream, we selected one sampling event from each season (rainy and dry). For each stream, only the first collection event of each season was used for the analyses (Table S2). The same dataset was used to investigate the metacommunity structure of fish based on taxonomic facet (see Martins et al., 2024). A single individual from the Chondrichthyes class (*Potamotrygon* aff. *orbignyi*, see Appendix S3), one of the three classes of fish that occur in the Amazon basin, was collected during one of the sampling events. *Potamotrygon* is a genus of rays that occurs in lakes and rivers in all tributaries of the Amazon Basin (Sanches et al., 2021; Van der Sleen & Zanata, 2017). Thus, the exclusion of this species from the phylogeny and analyses was necessary to maintain the focus on the ecosystem of small headwater streams. The inclusion of a class with a wide distribution throughout the studied basin, but restricted to larger bodies of water, could have introduced a bias in the analysis of the phylogenetic relationships among the fish species that are truly characteristic of the analyzed environments. Thus, the exclusion of *Potamotrygon* aff. *orbignyi* ensured a more precise focus on the ecosystem of small headwater streams.

FD (Petchey & Gaston, 2002) was based on a species' traits dendrogram and measures the total branch length of species present in each sampling unit. For this purpose, with the matrix of species and traits (represented by the first six PCA axes), we calculated the species dissimilarities using the Euclidean distance using basic R functions. Subsequently, a cluster analysis was performed to create a dendrogram using the '*hclust*' function from the stats package. This dendrogram was then transformed into a file of class '*phylo*' using the '*as.phylo*' function from the ape package. Finally, the FD value was calculated using the *pd* function from the picante package. The PD (Faith, 1992) was calculated using the '*pd*' function in the R package '*picante*' (Kembel et al., 2010). PD is a measure of the total evolutionary history represented by all the species in a community, calculated by adding up the lengths of the branches that connect them (Faith, 1992).

We applied the LCBd approach (Legendre & De Cáceres, 2013) to calculate the functional and phylogenetic uniqueness of the ichthyofauna of streams in the Xingu River basin. For this, we calculated the LCBd values following the methods proposed by Nakamura et al. (2020), who expanded the original framework of local contribution to beta diversity

(LCBD) to portray variation in the phylogenetic and functional facets of communities. As in the original method, locations with high values are more ecologically exclusive, that is, more unique. They may host unique clades and have species with unique functional attributes compared to other local communities. Consequently, these locations contribute more to the total beta diversity of a region compared to those with lower values. To determine the functional local contribution to β diversity (XLCBD) and phylogenetic local contribution to β diversity (PLCBD), which were calculated with the raw data approach, we used the code available from Zenodo: [<https://doi.org/10.5281/zenodo.3817980>] (Nakamura et al., 2020).

For each diversity index (FD, PD, XLCBD, and PLCBD), we tested the effects of spatial factors, the environment, and connectivity using multiple regression together with variation partitioning analysis (Legendre & Legendre, 1998; Peres-Neto et al., 2006). First, for a given diversity response, factors from a predictor set (i.e., spatial, environmental, and connectivity) were selected using forward selection (Blanchet et al., 2008). The selection proceeded only if the overall model, which included the response and all factors from a set, was significant ($\alpha = 0.1$). Variables were selected if they increased the adjusted R^2 of the models, were significant ($\alpha = 0.05$), and the adjusted R^2 did not exceed that of the overall model. Before building the models, the environmental predictor variables (except pH) and connectivity were transformed into log (log $x+1$) and standardized to zero mean and unit variance. Also, before the construction of the models, the variables were tested for multicollinearity. For this, we used the Pearson correlation coefficient, excluding a correlated variable until all correlation pairs were < 0.7 . For both seasons, catchment area and Link were correlated (Pearson $r = 0.92$), so we kept only Link in the analyses. Also, in the rainy season, we removed mean depth due to its correlation with Link (Pearson $r = 0.72$). For the dry season, mean canopy cover and Aquatic plants were correlated (Pearson $r = -0.91$), so we kept only mean canopy cover (Table S4).

We applied a partial linear regression-based variation partitioning structure to obtain the unique and shared contributions of predictor variables (i.e., environmental, connectivity, and spatial) in explaining diversity patterns (Legendre & Legendre, 2012). The components obtained were as follows: (1) explanation of solely the environmental variables (local and landscape); (2) explanation of solely the connectivity; (3) explanation of solely the spatial component; (4) explanation of the environment with the effect of connectivity and spatial; (5) explanation of connectivity with the effect of environmental variables and spatial; (6) explanation of the spatial component with the effect of environmental variables and connectivity; (7) shared component between environment, connectivity, and spatial; and (8)

residuals. For this, the ‘*varpart*’ function of the ‘*vegan*’ package was applied to each diversity index (FD, PD, XLCBD, PLCBD) as a function of the selected predictor variables. The significance of each fraction of the explained variation was then tested by ANOVA (except for fractions; (7) shared component among environment, connectivity, and spatial; (8) residuals). Finally, to explore possible spatial congruence between different facets of the diversity of fish assemblages, we used Pearson’s correlation.

Results

The selected datasets for the analyses (one event from the dry season and one event from the rainy season) contained 7,953 ray-finned fishes, representing 88 species, 25 families and six orders. Sixty-one species were collected during both sampling periods. In the rainy season, 77 species were collected, 16 of which were unique. For the dry season sampling, 72 species were detected, 11 of which were exclusive. The most abundant species was *Knodus aff. savanensis* in both seasons (for more information, see Table S3).

The correlation between the indices varied considerably between the two seasons (Table 2 and see Table S5). FD and PD were strongly correlated in both collection seasons. On the other hand, the values of PLCBD and XLCBD exhibited slight spatial congruence during the rainy season (Spearman’s correlation = 0.43) and a lower correlation among all comparisons in the dry season (Spearman’s correlation = 0.02).

Table 2 Results of Spearman’s correlation among diversity indices calculated for fish assemblages sampled during the rainy and dry season. Functional diversity (FD), phylogenetic diversity (PD), phylogenetic local contribution to β diversity (PLCBD), functional local contribution to β diversity (XLCBD). High correlation (>0.7), medium correlation (0.3-0.7) and low correlation (<0.3).

Diversity indices rainy	Rainy season				Dry season			
	FD	PD	XLCBD	PLCBD	FD	PD	XLCBD	PLCBD
FD	1				1			
PD	0.95	1			0.98	1		
XLCBD	-0.32	-0.31	1		-0.14	-0.09	1	
PLCBD	-0.51	-0.49	0.43	1	-0.46	-0.48	0.02	1

The analyzed facets of diversity (functional and phylogenetic) were influenced by a combination of environmental factors and connectivity (TableS6). Furthermore, the spatial structure (distance between streams) did not contribute to the variation in the values of the

analyzed indices. The final models, except for the PLCBD models, included only pure environmental or connectivity variables. PD and FD, indices that are highly correlated, were explained exclusively by Link during the rainy period and by a combination of local environmental variables during the dry period (Figure 2 and 3, Table S6). The XLCBD values were exclusively associated with environmental conditions (Figure 4, Table S6). During the rainy period, local environmental variables (conductivity, pH, and depth) were responsible for 30% of the variation in the XLCBD values. However, during the dry period, the catchment slope, a catchment-scale variable, explained 38% of the variation in XLCBD values. The PLCBD values were jointly explained by the environment and connectivity. In the rainy period, this joint explanation accounted for 16%, while in the dry period, it increased to 39% (Figure 5, Table S6).

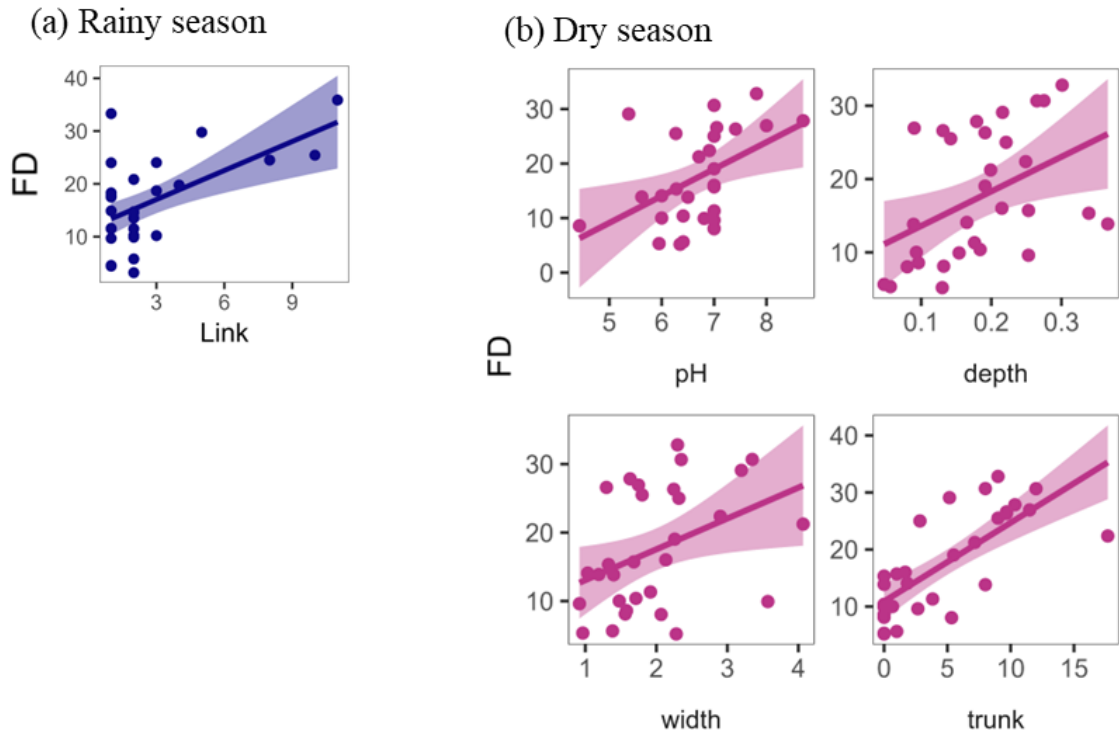


Figure 2 Relationships between functional diversity (FD) and selected variables in the global models including environmental and connectivity variables selected by the forward selection analysis. (a) Models for the rainy season, and (b) models for the dry season.

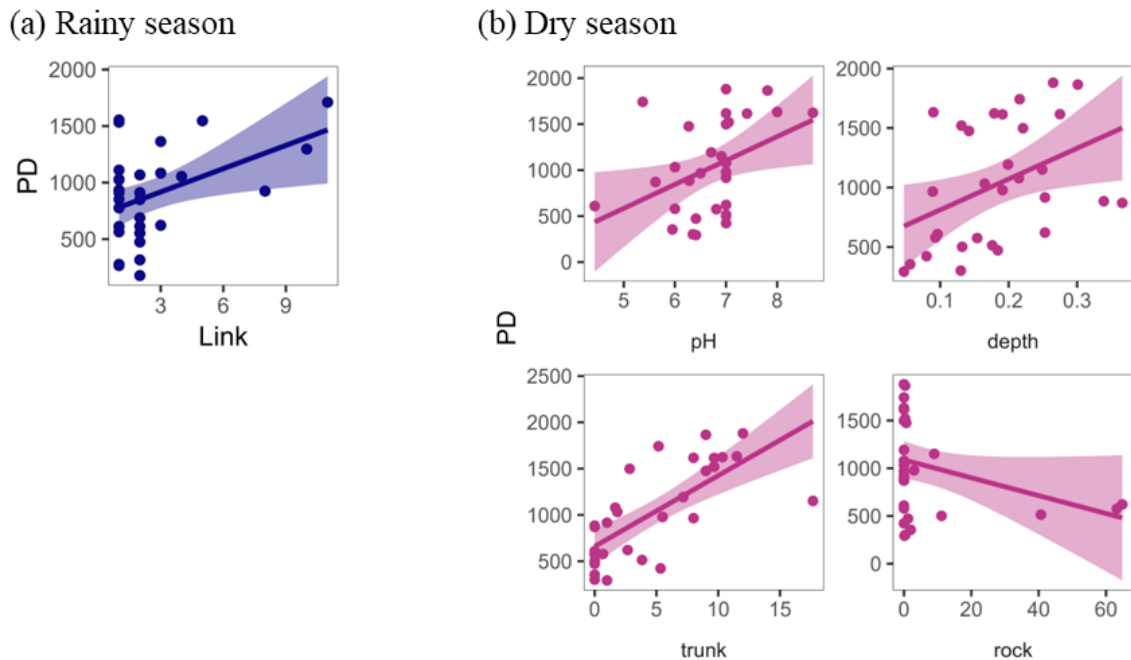


Figure 3 Relationships between phylogenetic diversity (PD) and selected variables in the global models including environmental and connectivity variables selected by the forward selection analysis. (a) Models for the rainy season, and (b) models for the dry season.

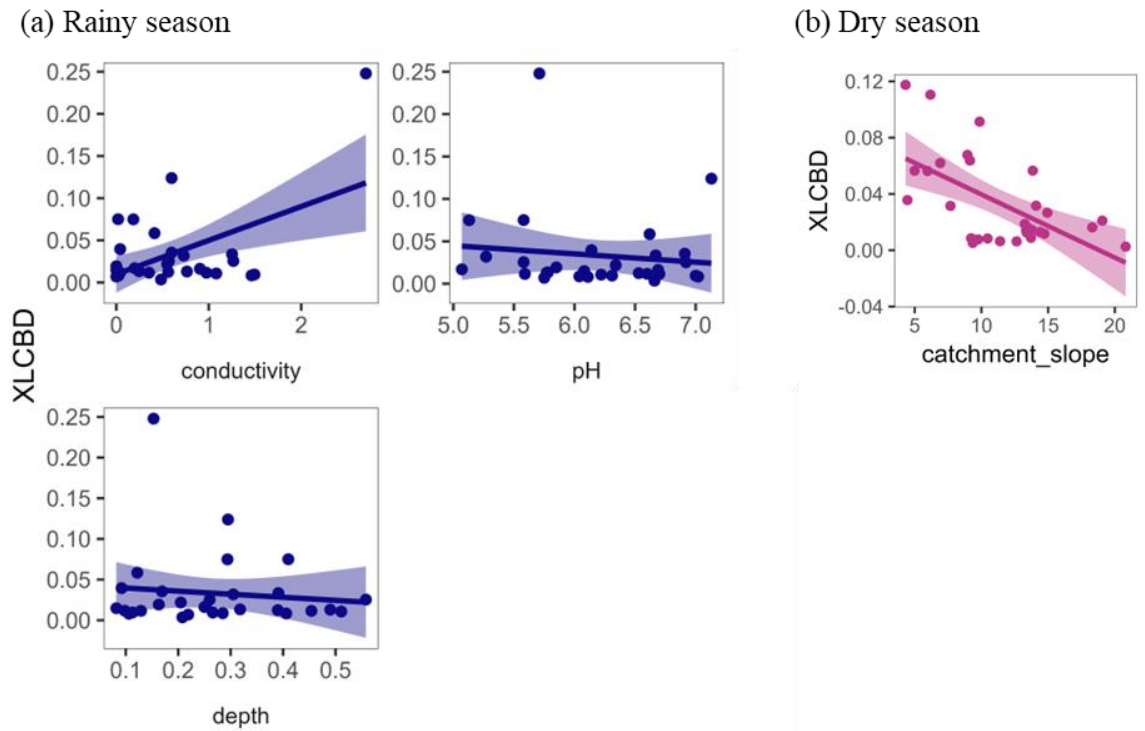


Figure 4 Relationships between functional local contribution to β diversity (XLCBD) and selected variables in the global models including environmental and connectivity variables selected by the forward selection analysis. (a) Models for the rainy season, and (b) models for the dry season.

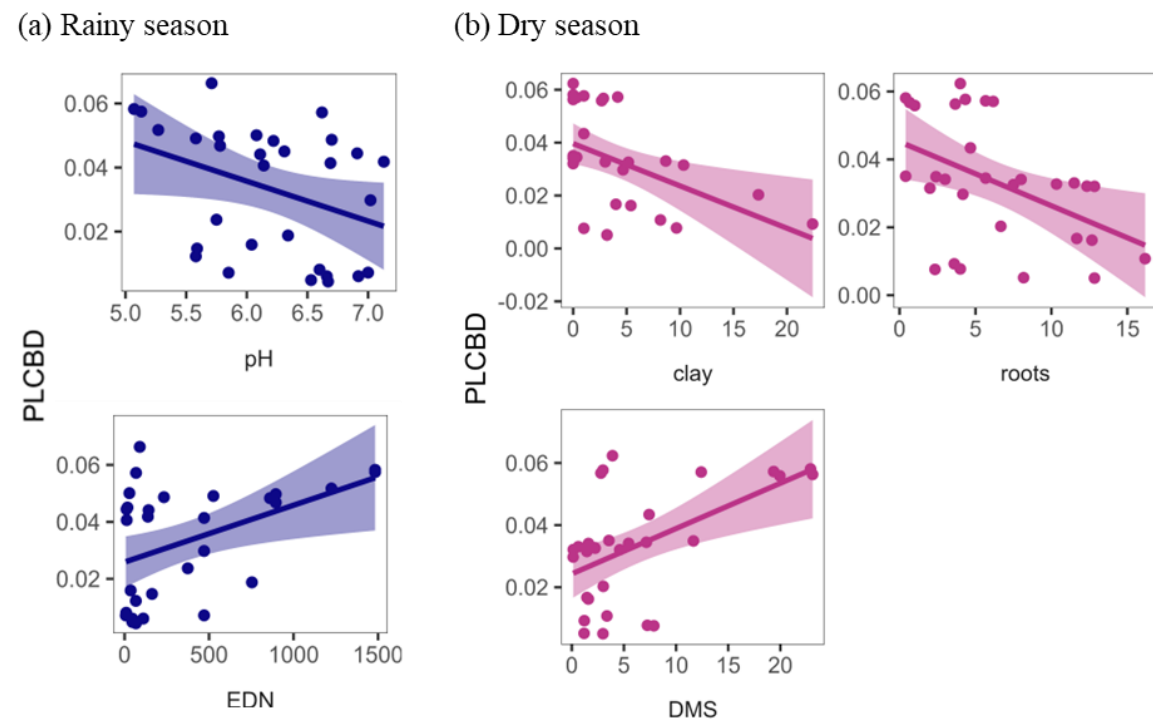


Figure 5 Relationships between phylogenetic local contribution to β diversity (PLCBD) and selected variables in the global models including environmental and connectivity variables selected by the forward selection analysis. (a) Models for the rainy season, and (b) models for the dry season.

Discussion

We investigated the effects of environmental conditions, connectivity, and space on local components of the functional and phylogenetic diversities of fish assemblages in headwater streams of the Xingu River basin, eastern Amazon. Our findings suggest that patterns of FD and PD, as well as some variation in the phylogenetic uniqueness of the fish assemblages, are a result of local environmental conditions and the connectivity of streams in the drainage network. However, functional uniqueness was exclusively associated with environmental conditions. Therefore, the diversity and ecological uniqueness of fish assemblages in the sampled streams appear to be directly linked to niche-based processes. Furthermore, the sets of predictors responsible for the index patterns varied between the rainy and dry seasons, emphasizing the effect of seasonality on the ichthyofauna of Amazonian *terra-firme* streams (Borba et al., 2021; Espírito-Santo et al., 2009; Espírito-Santo & Zuanon, 2017).

The predictors of functional and phylogenetic uniqueness in the analyzed assemblages varied slightly between seasonal periods. Moreover, these differences became even more drastic when we compared the predictors of FD and PD of the streams studied. The level of additional information that different facets of diversity can provide for understanding the dynamics of biological community organization depends on a combination of factors (Heino & Tolonen, 2017; Zbinden et al., 2022). These include location (Burgad et al., 2019; Zbinden et al., 2022), environmental heterogeneity (Thomsen et al., 2022), spatial scale (Legendre, 2014), and the organism group (i.e., phylogenetic scale, Branco et al., 2020). These factors are determinants due to the evolutionary and ecological history of the study area (Castillo-Escrivà et al., 2017; Rodrigues-Filho et al., 2018). In addition, contemporary factors related to dispersal capacity and niche-based processes can vary depending on the spatial configuration and the taxonomic group analyzed (Heino, 2013b; Heino, Nokela, et al., 2015; Schmera et al., 2018; Tonkin et al., 2018). Therefore, generalizations about patterns should be made with caution (Heino & Tolonen, 2017; Zbinden et al., 2022).

Our findings partially supported our initial hypothesis that environmental factors are responsible for variations in FD and PD. During the dry season, FD and PD were explained by local environmental conditions. However, during the rainy season, the connectivity of water bodies was responsible for the observed patterns. In the dry season, PD decreased with the availability of rocks. Rocks are generally associated with environments with higher water velocity and a lower availability of organic matter such as coarse litter and wood (Benone et

al., 2017; Hoover et al., 2006). Streams with these characteristics have lower habitat availability for fish than less turbulent streams with greater availability of organic matter (Oliveira et al., 2012). In addition, few stream fish species are adapted to life in fast waters (Jaramillo-Villa et al., 2010). We found that pH, the availability of trunks, and channel depth were positively associated with FD and PD, as was channel width with FD. These results are consistent with previous studies that showed that changes in the functional structure of fish assemblages are related to local environmental conditions (Leitão et al., 2018; Roa-Fuentes et al., 2022; Teresa & Casatti, 2012). Channel width positively influences the FD of fish assemblages in streams (Carvalho et al., 2023), as an increase in channel width can lead to an increase in habitat heterogeneity, providing a greater variety of environments for fish species (Spurgeon et al., 2019). During the rainy season, an important part of the variation in FD values and a smaller proportion of PD values were explained by the number of unbranched flows upstream Link. We used Link as a variable that captures the availability of processes upstream from the sampling site (Shreve, 1966; Yan et al., 2011). However, our results suggested that this connectivity variable captured the entry of common fish species into larger downstream systems (e.g., *Bivibranchia velox*, *Ctenobrycon spilurus* and *Myloplus rubripinnis*). The composition of the ichthyofauna of smaller streams (1st and 2nd order) differs from that of larger streams (3rd order or more) (Mendonça et al., 2005). The headwater streams of Amazonia are heavily dependent on rainfall patterns and respond quickly to local precipitation (Espírito-Santo et al., 2009; Pazin et al., 2006). For streams in central Amazonia, predictable differences in the structure of fish assemblages were detected between the dry and rainy seasons, related to the use of temporary pools associated with stream channels during the rainy season (Espírito-Santo et al., 2009; Pazin et al., 2006). This seasonal pattern was not found in perennial streams in the Xingu River basin (Martins et al., 2022) the same streams analyzed in the present study. The large volume of water may have increased the connectivity of smaller streams with downstream stretches, resulting in the entry of common fish species from larger streams. Thus, these species may access these streams during the rainy season, temporarily inhabit these places during periods of high flow (e.g., mass effects; Leibold et al., 2004), and subsequently return to larger systems after the flow decreases.

Our second prediction was that functional uniqueness would be driven by environmental filtering and processes related to dispersal. Consequently, we anticipated that the values of functional uniqueness could vary significantly even among adjacent locations because communities respond to variations in environmental conditions and river connectivity (Martins et al., 2024; Poff, 1997). Furthermore, we expected functional

uniqueness to be spatially structured because part of the explanation for the distribution of taxa in communities would be driven by the spatially related dispersal and ecological drift (Hubbell, 2001; Vellend, 2010). However, our results supported only the first part, where the functional uniqueness of fish assemblages was influenced by environmental filtering. The headwater streams of the Amazon are heavily influenced by the local rainfall regime, where sudden high-flow events throughout the year are common due to increased rainfall (Espírito-Santo et al., 2009; Pazin et al., 2006). Both the hydrological variation and the high environmental heterogeneity are key factors in the organization of fish assemblages, as they act as filters for fish species and their characteristics (Landeiro et al., 2011; Poff, 1997; Zbinden & Matthews, 2017). Our results indicated that the relationships between the functional uniqueness of stream ichthyofauna and environmental variables may reflect this environmental filtering process. During the rainy season, functional uniqueness showed a negative association with average channel depth and basic pH but a positive association with water conductivity. An increase in stream depth provides a greater variety of micro-habitats (Gorman & Karr, 1978; Matthews, 1998), which in turn influences the selection of characteristics related to swimming, habitat preference and the use of food resources in local fish assemblages (Pease et al., 2012). In addition, water conductivity is expected to influence the occurrence of fish species, where in the same type of habitat, changes in conductivity values are responsible for the variation in local species composition (De Carvalho & Tejerina-Garro, 2018). According to our results for the rainy season, the locations with the highest functional uniqueness values were those that were shallower, with more basic pH, and with higher conductivity values. This uniqueness may be related to the loss of functional traits in these locations, as it is precisely in the rainy season that uniqueness showed a negative correlation with FD. During the dry season, functional uniqueness was negatively associated with catchment slope. These results reinforce the importance of catchment slope for determining the dynamics of fish assemblages in headwater streams in the Xingu River basin (Martins et al., 2024). For the assemblages studied, previous results detected that higher catchment slope values were responsible for the greater local abundance of active swimmers which occupied the middle and upper layers in stream channels. In contrast, locations with lower catchment slope values had a greater abundance of species with limited swimming capacity (Martins et al., 2024). Thus, higher catchment slope values may filter out species with low swimming capacity, making local assemblages more functionally unique.

Our third hypothesis predicted that phylogenetic uniqueness would be determined solely by spatial factors. In general, we expected that locations that could have lost species

over time, caused by, for example, environmental changes (e.g., Magalhães et al., 2021), might not have been recolonized due to the low connectivity of headwater streams (Heino, Melo, et al., 2015; Palheta et al., 2021; Vitorino Júnior et al., 2016) and the limited dispersal capacity of stream ichthyofauna (Castro, 1999; Mendonça et al., 2005). In addition, the fish species composition of these streams differed with increasing distance (Martins et al., 2024). Thus, our expectations were that these differences would be captured by phylogenetic uniqueness due to the effect of historical events on the phylogenetic structure (Leibold et al., 2010; Nakamura et al., 2020). Over larger extents, dispersal limitation becomes a more important factor in phylogenetic differences between communities due to historical effects (Graham & Fine, 2008; Leibold et al., 2010). Despite the distance of the studied streams (average distance = 152 km; range = 1.83–367 km) as a key factor for the structure of fish assemblages of these streams from the taxonomic facet (Martins et al., 2024). Our findings contradicted our initial hypothesis and demonstrated that the studied streams share a similar phylogenetic history without the loss of phylogenetic or functional information along the spatial gradient. This unique history experienced by the studied assemblages reinforces the effect of climatic and environmental stability experienced by Amazonian ichthyofauna (Oberdorff et al., 2019; Peres et al., 2010).

We sought to understand the underlying mechanisms of the organization of fish assemblages in headwater streams of the Xingu River basin, eastern Amazon. We explored the effects of environmental conditions, connectivity, and space on aspects of the functional and phylogenetic facets of ichthyofauna. We found that patterns of FD and PD diversity are related to local environmental conditions and the connectivity of water bodies in the drainage network, with marked seasonal differences. We also discovered that functional uniqueness was influenced by environmental filtering related to environmental variables at multiple scales. An important part of phylogenetic uniqueness was associated with the effect of local environmental conditions and the connectivity of water bodies in the drainage network. In general, our findings suggest that the diversity and ecological uniqueness of fish assemblages in headwater streams are directly linked to niche-based processes, highlighting the importance of environmental conditions in the selection of species with functional characteristics. Our results also indicated a narrow shared phylogenetic history among the studied streams, likely due to the effects of climatic and environmental stability experienced by Amazonian ichthyofauna over evolutionary time (Oberdorff et al., 2019; Peres et al., 2010).

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Author contributions

Conceptualisation: ARM, LUH and SVM. Developing methods: DAB, LMS and TG. Conducting the research: ARM and DAB. Data analysis & preparation of figures and tables: ARM. Data interpretation: ARM, LUH and SVM. Writing: all authors.

Data availability

The data that support the findings of this study are available upon request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Table S3. Summary of fish collection activities and environmental variables in each stream during the 12 sampling campaigns conducted between March 2012 and October 2014 in the region of Volta Grande do Xingu, Pará state, Brazilian Eastern Amazon. 1 = Sampling successfully performed; 2 = Streams that dried up or with no flow (isolated ponds); 3 = Very high-water volume (no conditions to perform standardized sampling); 4 = No access to the site (trail closed by vegetation or blocked road); 5 = Collection point had not yet been implemented; 6 = Collection point is no longer inventoried. * = Sampling selected in the rainy season; # = sampling selected during the dry season.

Stream	2012				2013				2014			
	Rainy season March/April	Dry season			Rainy season January	April	Dry season		Rainy season January/ February	April	Dry season	
		June	September/ October	November			July	October			July	October
ST01	1*	1#	2	2	1	1	1	2	2	1	1	2
ST02	1*	1#	2	2	1	1	1	1	1	1	1	2
ST03	1*	4	2	2	1	1	1#	1	1	1	1	1
ST04	1*	4	1#	2	6	6	6	6	6	6	6	6
ST05	1*	2	2	2	4	1	1#	2	2	4	2	2
ST06	1*	1#	1	1	1	1	1	1	1	1	1	1
ST07	1*	1#	1	1	1	1	1	1	1	1	1	1
ST08	1*	1#	1	1	1	1	1	1	1	1	1	1
ST09	1*	1#	1	1	6	6	6	6	6	6	6	6
ST10	1*	1#	1	1	1	1	1	1	1	1	1	1
ST11	1*	1#	2	2	2	1	1	2	2	1	1	2
ST12	1*	1#	2	2	1	3	1	1	1	1	1	1
ST13	1*	1#	1	2	1	3	1	1	1	3	1	1
ST14	1*	4	1#	1	1	1	4	1	1	4	1	1
ST15	1*	1#	1	2	1	6	6	6	6	6	6	6

ST16	1*	4	2	2	1	1	1#	2	1	4	1	2
ST17	1*	1#	2	2	1	1	1	1	1	1	1	1
ST18	1*	1#	2	2	1	4	4	2	4	4	2	2
ST19	1*	1#	1	1	1	1	1	1	1	1	1	1
ST20	1*	1#	1	1	1	1	1	1	1	1	1	1
ST21	1*	1#	1	2	1	1	1	1	1	1	1	1
ST22	5	1#	1	1	1*	1	1	1	1	1	1	1
ST23	4	1#	1	2	1*	1	1	1	1	1	1	1
ST24	5	5	5	5	1*	4	1#	1	1	4	1	2
ST25	4	1#	2	2	1*	4	1	1	1	4	1	1
ST26	4	1#	2	2	1*	4	1	1	1	4	1	1
ST27	5	5	5	2	1*	1	1#	1	1	1	1	1
ST28	4	1#	2	2	2	1	1	1	1	1	1	2
ST29	4	1#	2	2	1*	4	3	1	1	4	1	2
ST30	5	5	5	5	2	2	2	2	2	1*	1#	2

Table S4 The 12 ecomorphological traits used to functionally characterize fish species of streams from the region of Volta Grande do Xingu, Pará state, Brazilian Eastern Amazon, and their ecological significance.

Ecomorphological trait	Code	Calculation	Ecological meaning	Reference
Oral-gape shape	Osh	$\frac{Md}{Mw}$	Method to capture food item	Karpouzi & Stergiou, 2003
Oral-gape position	Ops	$\frac{Mo}{Hd}$	Feeding strategy in the water column	Villéger et al., 2010 adapted from Sibbing & Nagelkerke, 2001
Eye size	Edst	$\frac{Ed}{Hd}$	Prey detection	Villéger et al., 2010 adapted from Boyle & Horn, 2000
Eye position	Eps	$\frac{Eh}{Hd}$	Vertical position in the water column	Gatz, 1979
Body transversal shape	Bsh	$\frac{Bd}{Bw}$	Vertical position in the water column and hydrodynamics	Sibbing & Nagelkerke, 2001
Body transversal surface	Bsf	$\frac{\ln \left[\left(\frac{\pi}{4} * Bw * Bd \right) + 1 \right]}{\ln (Mass + 1)}$	Distribution of mass throughout the body for hydrodynamics	Villéger et al., 2010
Pectoral-fin position	PFps	$\frac{PFi}{PFb}$	Pectoral-fin use for maneuverability	Dumay et al., 2004
Aspect ratio of the pectoral fin	PFar	$\frac{PFl^2}{PFs}$	Pectoral fin propulsion	Villéger et al., 2010 adapted from Fulton et al., 2001
Caudal-peduncle throttling	CPt	$\frac{CFd}{CPd}$	Swimming efficiency by reducing water resistance	Webb 1984
Aspect ratio of the caudal fin	CFar	$\frac{CFd^2}{CFs}$	Propulsion and steering by caudal fin	Webb 1984

Fins surface ratio	Frt	$\frac{2 * PFs}{CFs}$	Main type of propulsion	Villéger et al., 2010
Mass	logN	log (Mass+1)	Metabolism, endurance, and swimming ability	Villéger et al., 2010

Table S3. List of fish species sampled in 30 streams in the region of Volta Grande do Xingu, state of Pará, Brazilian Eastern Amazon. Occurrence refers to the total number of streams where the species were found.

Order	Family	Species	Rain	Dr	Occurrenc
Characiformes	Anostomidae	<i>Leporinus cf. granti</i> Eigenmann, 1912	x	x	2
		<i>Leporinus friderici</i> (Bloch, 1794)	x	x	5
		<i>Leporinus torrenticola</i> Birindelli, Teixeira & Britski 2016	x		2
	Bryconidae	<i>Brycon falcatus</i> Müller & Troschel, 1844	x	x	2
	Characidae	<i>Astyanax anterior</i> Eigenmann 1908	x		2
		<i>Astyanax gr. bimaculatus</i> (Linnaeus, 1758)	x	x	22
		<i>Creagrutus cf. ignotus</i> Vari & Harold 2001	x		2
		<i>Ctenobrycon spilurus</i> (Valenciennes, 1850)	x		1
		<i>Hemigrammus bellottii</i> (Steindachner, 1882)		x	1
		<i>Hemigrammus ocellifer</i> (Steindachner, 1882)		x	1
		<i>Hemigrammus</i> sp. “collettii”	x	x	11
		<i>Hyphessobrycon copelandi</i> Durbin, 1908	x	x	3
		<i>Hyphessobrycon heterorhabdus</i> (Ulrey, 1894)	x	x	2

	<i>Hyphessobrycon juruna</i> Faria, Lima & Bastos 2018	x	x	3
	<i>Hyphessobrycon</i> sp. “faixa negra”		x	2
	<i>Jupiaba polylepis</i> (Günther, 1864)	x	x	5
	<i>Knodus</i> aff. <i>savannensis</i>	x	x	17
	<i>Moenkhausia celibela</i> Marinho & Langeani, 2010	x	x	4
	<i>Moenkhausia comma</i> Eigenmann, 1908	x	x	7
	<i>Moenkhausia oligolepis</i> (Günther, 1864)	x	x	22
	<i>Moenkhausia pirauba</i> Zanata, Birindelli & Moreira, 2010	x	x	6
	<i>Moenkhausia xinguensis</i> (Steindachner, 1882)	x		1
	<i>Phenacogaster</i> aff. <i>calverti</i> (Fowler 1941)	x	x	1
	<i>Phenacogaster</i> aff. <i>napoatilis</i> Lucena & Malabarba 2010	x	x	7
	<i>Poptella fortispina</i> Garcia-Ayala & Benine 2023	x		1
	<i>Poptella brevispina</i> Reis, 1989	x	x	5
	<i>Serrapinnus tocantinensis</i> Malabarba & Jerep 2014	x	x	2
	<i>Tetragonopterus argenteus</i> Cuvier, 1816	x		1
	<i>Tetragonopterus chalceus</i> Spix & Agassiz, 1829	x		1
Crenuchidae	<i>Characidium</i> aff. <i>zebra</i> Eigenmann, 1909	x	x	9
	<i>Microcharacidium</i> aff. <i>weitzmani</i> Buckup, 1993	x	x	2
Curimatidae	<i>Cyphocharax gouldingi</i> Vari, 1992	x	x	3
Erythrinidae	<i>Erythrinus erythrinus</i> (Bloch & Schneider, 1801)	x	x	12
	<i>Hoplerythrinus unitaeniatus</i> (Spix & Agassiz, 1829)	x	x	6

		<i>Hoplias curupira</i> Oyakawa & Mattox, 2009		x	1
		<i>Hoplias malabaricus</i> (Bloch, 1794)	x	x	22
	Hemiodontidae	<i>Bivibranchia velox</i> (Eigenmann & Myers, 1927)	x		1
	Iguanodectidae	<i>Bryconops</i> aff. <i>caudomaculatus</i> (Günther, 1864)	x	x	1
		<i>Bryconops</i> aff. <i>magoi</i> Chernoff & Machado-Allison, 2005	x		1
		<i>Bryconops affinis</i> (Günther, 1864)	x	x	6
		<i>Bryconops melanurus</i> (Bloch, 1794)	x	x	2
		<i>Iguanodectes rachovii</i> Regan, 1912	x	x	2
	Lebiasinidae	<i>Copella arnoldi</i> (Regan, 1912)	x	x	7
		<i>Pyrrhulina</i> sp. N	x	x	4
	Prochilodontidae	<i>Prochilodus nigricans</i> Spix & Agassiz, 1829		x	1
	Serrasalminidae	<i>Myloplus rubripinnis</i> (Müller & Troschel, 1844)	x		1
Cyprinodontiformes	Rivulidae	<i>Anablepsoides xinguensis</i> (Costa, 2010)		x	14
		<i>Melanorivulus rubroreticulatus</i> Costa, Amorim & Bragança, 2014		x	1
	Poeciliidae	<i>Pamphorichthys araguiensis</i> Costa 1991	x		1
Gymnotiformes	Gymnotidae	<i>Gymnotus carapo</i> Linnaeus, 1758	x	x	13
		<i>Gymnotus coropinae</i> Hoedeman, 1962	x	x	2
	Hypopomidae	<i>Brachyhypopomus</i> aff. <i>regani</i> Crampton, de Santana, Waddell & Lovejoy 2017		x	3
		<i>Brachyhypopomus beebei</i> (Schultz, 1944)	x	x	11
		<i>Microsternarchus</i> aff. <i>bilineatus</i> Fernández-Yépez, 1968	x	x	2

Myliobatiformes	Rhamphichthyidae	<i>Gymnorhamphichthys rondoni</i> (Miranda Ribeiro, 1920)	x	x	8
		<i>Steatogenys duidae</i> (La Monte, 1929)		x	1
	Sternopygidae	<i>Eigenmannia</i> aff. <i>trilineata</i> López & Castello, 1966	x	x	9
		<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	x	x	2
	Potamotrygonidae	<i>Potamotrygon</i> aff. <i>orbignyi</i> (Castelnau, 1855)		x	1
	Perciformes	<i>Aequidens tetramerus</i> (Heckel, 1840)	x	x	21
		<i>Apistogramma geophyra</i> Kullander, 1980	x	x	2
		<i>Apistogramma</i> sp.	x	x	8
		<i>Apistogramma</i> sp. tracejado	x	x	4
		<i>Apistogramma</i> sp. vielfleck		x	1
		<i>Crenicichla</i> gr. <i>saxatilis</i> (Linnaeus, 1758)	x	x	15
		<i>Satanoperca</i> aff. <i>jurupari</i> (Heckel, 1840)	x	x	2
Siluriformes	Auchenipteridae	<i>Auchenipterichthys punctatus</i> (Valenciennes, 1840)		x	1
		<i>Tatia</i> aff. <i>gyrina</i> (Eigenmann & Allen, 1942)	x	x	1
		<i>Tatia intermedia</i> (Steindachner, 1877)	x	x	2
		<i>Trachelyopterus porosus</i> Eigenmann & Eigenmann, 1888	x		1
	Callichthyidae	<i>Callichthys callichthys</i> (Linnaeus, 1758)	x	x	9
		<i>Corydoras</i> cf. <i>aeneus</i> (Gill, 1858)	x	x	11
		<i>Megalechis picta</i> (Müller & Troschel, 1849)	x	x	9
	Cetopsidae	<i>Cetopsidium orientale</i> (Vari, Ferraris & Keith 2003)	x		1
		<i>Denticetopsis epa</i> Vari, Ferraris & de Pinna 2005	x	x	2

		<i>Helogenes marmoratus</i> Günther, 1863	x	x	2
	Heptapteridae	<i>Imparfinis</i> aff. <i>hasemani</i> Steindachner, 1917	x	x	3
		<i>Phenacorhamdia</i> sp.	x	x	3
		<i>Pimelodella</i> sp. “faixa grossa”	x	x	12
		<i>Rhamdia quelen</i> (Quoy & Gaimard 1824)	x	x	12
	Loricariidae	<i>Ancistrus</i> sp. “bola”	x	x	8
		<i>Curculionichthys</i> sp. “alto”	x		2
		<i>Hypostomus</i> aff. <i>plecostomus</i> (Linnaeus, 1758)	x	x	6
		<i>Hypostomus hemicochliodon</i> Kner, 1854	x		2
		<i>Otocinclus</i> cf. <i>hasemani</i> Steindachner 1915	x	x	6
		<i>Rineloricaria lanceolata</i> (Günther, 1868)	x	x	7
		<i>Rineloricaria</i> sp.	x	x	5
	Trichomycteridae	<i>Ituglanis</i> aff. <i>amazonicus</i> (Steindachner 1882)	x	x	7
Synbranchiformes	Synbranchidae	<i>Synbranchus</i> aff. <i>madeira</i> Rosen & Rumney, 1972	x	x	14

Table S4. Characterization of physico-chemical, landscape, and connectivity variables of the headwater streams sampled in in the region of Volta Grande do Xingu, Pará state, Brazilian Eastern Amazon. Values displayed refer to the minimum (Min) and maximum (Max), mean, standard deviation (SD), and the coefficient of variation (CV) for samples selected for the rainy and dry seasons. * = Variables excluded after analysis of multicollinearity. Catchment area and stream link magnitude (Link) (Pearson $r = 0.92$). In the rainy season, mean depth correlated with stream link magnitude (Link) (Pearson $r = 0.72$). In the dry season, mean canopy cover and aquatic plants were correlated (Pearson $r = -0.91$).

Rainy						Dry					
Variables	Min	Max	Mean	SD	CV (%)	Variables	Min	Max	Mean	SD	CV (%)
pH	5.07	7.13	6.19	0.59	9.48	pH	4.43	8.70	6.70	0.81	12.03
Temperature (°C)	24.00	29.09	25.75	1.33	5.16	Temperature (°C)	22.80	30.10	25.95	2.06	7.95
Conductivity (mS/cm)	0.00	2.70	0.58	0.61	105.02	Conductivity (mS/cm)	0.00	0.16	0.05	0.04	85.95
Dissolved oxygen (mg/l)	4.14	9.72	7.90	1.47	18.58	Dissolved oxygen (mg/l)	1.15	8.81	5.29	1.98	37.50
*Mean depth (m)	0.08	0.56	0.27	0.14	50.82	Mean depth (m)	0.05	0.37	0.18	0.08	44.84
Mean width (m)	1.20	4.88	2.68	0.94	35.13	Mean width (m)	0.92	4.07	1.99	0.79	39.55
Mean canopy cover (%)	4.57	93.84	73.21	29.89	40.83	Mean canopy cover (%)	1.10	94.95	66.34	26.17	39.44
Sand (%)	1.67	88.75	39.67	21.50	54.20	Sand (%)	5.17	79.60	30.54	22.89	74.93
Clay (%)	0.00	22.00	5.73	6.59	115.00	Clay (%)	0.00	22.40	3.95	5.37	135.87
Gravel (%)	0.00	62.00	6.55	13.86	211.51	Gravel (%)	0.00	58.17	11.39	13.67	120.05
Fine litter (%)	0.00	77.17	14.27	19.23	134.76	Fine litter (%)	0.00	41.83	16.57	11.13	67.14
Coarse litter (%)	0.00	47.00	13.89	11.81	85.02	Coarse litter (%)	0.80	42.83	16.90	12.59	74.48
Aquatic plants (%)	0.00	38.13	2.82	7.48	265.58	*Aquatic plants (%)	0.00	17.33	3.01	5.76	191.69
Roots (%)	0.00	31.88	7.95	8.22	103.40	Roots (%)	0.40	16.17	6.29	4.42	70.21
Rock (%)	0.00	54.75	4.20	11.79	280.81	Rock (%)	0.00	64.83	6.57	17.40	265.01
Trunk (%)	0.00	67.67	4.92	12.88	261.69	Trunk (%)	0.00	17.67	4.78	4.77	99.79
Forest cover (%)	0.00	100.00	49.59	35.10	70.77	Forest cover (%)	0.00	100.00	49.59	35.10	70.77
Catchment slope (%)	4.32	20.81	11.41	4.26	37.28	Catchment slope (%)	4.32	20.81	11.41	4.26	37.28
*Catchment area (km ²)	0.25	17.16	3.35	4.16	124.15	*Catchment area (km ²)	0.25	17.16	3.35	4.16	124.15
EDN (km)	7.35	1482.70	373.26	449.83	120.52	EDN (km)	7.35	1482.70	373.26	449.83	120.52
DMS (km)	0.13	23.09	6.18	6.80	109.95	DMS (km)	0.13	23.09	6.18	6.80	109.95
Link	1.00	11.00	2.60	2.62	100.80	Link	1.00	11.00	2.60	2.62	100.80
D.Link	2.00	117.00	12.20	23.27	190.71	D.Link	2.00	117.00	12.20	23.27	190.71

Table S5 For each stream the diversity values observed for functional diversity (PD), phylogenetic diversity (PD), functional local contribution to β diversity (XLCBD) values and phylogenetic local contribution to β diversity (PLCBD).

Rainy season					Dry season				
Stream	FD	PD	XLCBD	PLCBD	Stream	FD	PD	XLCBD	PLCBD
ST01	25.431	1296.605	0.009	0.007	ST01	8.038	422.899	0.021	0.008
ST02	24.509	924.394	0.008	0.030	ST02	19.038	978.414	0.009	0.056
ST03	5.780	316.133	0.016	0.041	ST03	9.927	575.408	0.016	0.058
ST04	14.885	912.021	0.033	0.004	ST04	22.376	1151.354	0.032	0.017
ST05	11.526	775.754	0.022	0.019	ST05	8.584	609.049	0.057	0.009
ST06	9.883	474.369	0.011	0.048	ST06	11.322	513.991	0.013	0.056
ST07	11.498	612.224	0.013	0.050	ST07	15.717	916.640	0.014	0.057
ST08	10.186	622.047	0.013	0.047	ST08	10.009	579.438	0.012	0.043
ST09	35.878	1710.900	0.025	0.012	ST09	30.687	1616.847	0.027	0.032
ST10	20.839	1068.059	0.012	0.015	ST10	30.667	1880.672	0.003	0.008
ST11	18.296	1110.803	0.035	0.044	ST11	26.945	1632.297	0.009	0.016
ST12	33.303	1534.160	0.004	0.006	ST12	27.850	1623.261	0.006	0.020
ST13	19.770	1054.702	0.012	0.005	ST13	32.811	1865.586	0.006	0.011
ST14	11.498	612.224	0.008	0.044	ST14	15.337	885.095	0.014	0.062
ST15	14.721	849.457	0.124	0.042	ST15	13.878	870.530	0.064	0.033
ST16	17.743	934.726	0.012	0.049	ST16	5.322	354.955	0.032	0.035
ST17	11.570	852.327	0.058	0.057	ST17	13.830	965.553	0.056	0.033
ST18	17.712	1024.312	0.025	0.006	ST18	14.084	1032.407	0.068	0.032
ST19	17.502	1029.210	0.017	0.058	ST19	16.019	1078.510	0.062	0.057
ST20	13.529	688.637	0.075	0.057	ST20	25.009	1498.384	0.008	0.005
ST21	4.549	265.879	0.032	0.052	ST21	8.115	501.615	0.008	0.034
ST22	4.414	276.511	0.015	0.050	ST22	9.610	621.280	0.016	0.057
ST23	23.987	1553.813	0.010	0.045	ST23	26.597	1520.148	0.005	0.005
ST24	3.183	177.477	0.248	0.066	ST24	5.190	301.884	0.118	0.034

ST25	14.507	911.402	0.019	0.007	ST25	25.501	1475.593	0.057	0.032
ST26	18.691	1083.819	0.007	0.024	ST26	29.094	1742.065	0.036	0.033
ST27	9.682	564.776	0.012	0.008	ST27	10.386	472.303	0.019	0.035
ST28	24.032	1363.601	0.075	0.049	ST28	26.319	1614.889	0.091	0.034
ST29	29.771	1546.873	0.009	0.016	ST29	21.236	1192.620	0.111	0.030
ST30	10.237	552.383	0.040	0.041	ST30	5.632	293.537	0.013	0.058
Minimum	3.183	177.477	0.004	0.004	Minimum	5.190	293.537	0.003	0.005
Maximum	35.878	1710.900	0.248	0.066	Maximum	32.811	1880.672	0.118	0.062
Mean	16.304	889.987	0.033	0.033	Mean	17.504	1026.241	0.033	0.033
Standard Deviation	8.303	407.493	0.048	0.020	Standard deviation	8.797	512.083	0.032	0.018

The functional diversity (FD) of the streams during the rainy season varied between 3.18 and 35.87 (mean FD = 16.30, SD = 8.30), while that during the dry season ranged from 5.19 to 32.81 (mean FD = 17.50, SD = 8.79). During the rainy period, the phylogenetic diversity (PD) of the streams varied between 177.48 and 1710.90 (mean PD = 889.99, SD = 407.49). For the dry season, the variation ranged from 293.54 to 1880.67 (mean PD = 1026.24, SD = 512.08). The functional local contribution to β diversity during the rainy period varied between 0.0036 and 0.2479 (mean XLCBD = 0.0333, SD = 0.0482), while for the dry season, it ranged from 0.0026 to 0.1175 (mean XLCBD = 0.0333, SD = 0.0320). The phylogenetic local contribution to β diversity during the rainy period varied between 0.0044 and 0.0663 (mean PLCBD = 0.0333, SD = 0.0201), while for the dry season, it ranged from 0.0050 to 0.0623 (mean PLCBD = 0.0333, SD = 0.0182).

Table S6. Results of variation partitioning analyses of environmental, connectivity, and spatial predictors against functional diversity (FD), phylogenetic diversity (PD), functional local contribution to β diversity (XLCBD) and phylogenetic local contribution to β diversity (PLCBD) values for fish assemblages of the streams sampled in the region of Volta Grande do Xingu, state of Pará, Brazilian Eastern Amazon.

Environmental, Connectivity and spatial predictors	FD rainy			FD dry			PD rainy			PD dry		
	R2 adj (%)	<i>p</i>	SV	R2 adj (%)	<i>p</i>	SV	R2 adj (%)	<i>p</i>	SV	R2 adj (%)	<i>p</i>	SV
Environ. Connectivity Spatial												
Pure environ.				0.707	0.001*	pH, CD, CW, trunk				0.710	0.001*	pH, CD, trunk, rock
Pure connectivity	0.311	0.001*	Link				0.166	0.001	Link			
Pure spatial												
Total												
Residuals												
	XLCBD rainy			XLCBD dry			PLCBD rainy			PLCBD dry		
	R2 adj (%)	<i>p</i>	SV	R2 adj (%)	<i>p</i>	SV	R2 adj (%)	<i>p</i>	SV	R2 adj (%)	<i>p</i>	SV
Environ. Connectivity Spatial							0.101 0.170	0.047 pH 0.013 EDN		0.336 0.271	0.003* 0.002*	clay, roots DMS
Pure environ.	0.305	0.030*	WC, pH CD	0.385	0.0001*	CS	-0.010	0.388		0.123	0.031*	
Pure connectivity							0.060	0.096		0.057	0.094	
Pure spatial												
Total							0.161 0.839	0.037		0.393 0.607	0.0011	
Residuals												

SV = variables selected by the forward selection analysis, CW= channel width, CD= channel depth, CS= catchment slope, WC = water conductivity, DMS= distance from the mainstream, EDN= The extension of the drainage network, Link = stream link magnitude



Drought intensification drives patterns of temporal beta diversity of fish assemblages in tropical streams

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Abstract

Climate change is altering hydrological regimes worldwide, leading to more frequent and prolonged droughts in various regions. These shifts have profound effects on aquatic ecosystems, particularly headwater streams, which are highly susceptible to drying. Understanding how these disturbances influence the temporal dynamics of aquatic communities is crucial for conservation efforts. This study examines the impact of extreme drought events on the temporal β -diversity of fish assemblages in Amazonian headwater streams. Based on samples collected over 11 years (2012-2023), in a stream system that includes perennial water bodies and streams that experienced flow loss, temporal β -diversity and its components (turnover and nestedness) were calculated. In both types of streams (perennial and those that suffered flow loss), the species turnover component was the main driver of the temporal beta diversity of these assemblages. However, despite turnover being the main component in all scenarios, drought events intensify this mechanism. The recolonization process after disturbances generates a new species composition, where there is no nestedness in these assemblages, but rather a replacement process. These results highlight the vulnerability of Amazonian headwater stream fish communities to drought-induced disturbances. As climate change intensifies, with predictions of increased drought frequency and severity in the Eastern Brazilian Amazon, these findings raise concerns about the long-term stability and persistence of the region's unique aquatic biodiversity.

Keywords: Extreme events, fish fauna, disturbance, community ecology, null models

Introduction

More than 50% of the global river network is constituted by aquatic systems that experience periods of no flow at some point within the seasonal cycle (Datry et al., 2014). This phenomenon has generated growing concern, especially considering projections for increased extreme weather events, such as droughts and floods, attributable to climate change (IPCC, 2023; Prudhomme et al., 2014). The intensification of extreme drought events is anticipated to lead to a shift in numerous perennial streams, causing them to become intermittent (Döll & Schmied, 2012). This transition from perennial to intermittent flow regimes can fragment the water network, resulting in habitat loss for aquatic organisms and subsequent declines in biodiversity (Lake, 2011; Sabater et al., 2018; Vander Vorste et al., 2020). Consequently, biotic homogenization may occur, as drought-sensitive species disappear, leaving local communities dominated by those adapted to drought conditions (Lake, 2011; Leigh & Datry, 2017).

The Amazonian ichthyofauna demonstrates vulnerability to changes in environmental conditions (Martins et al., 2022; Röpké et al., 2017), which can be partly attributed to the higher climatic and environmental consistency that has characterized this fauna throughout its evolutionary development (Oberdorff et al., 2019; Peres et al., 2010). Initial studies demonstrate that the loss of flow in headwater streams of the Amazon has a significant impact on the composition of fish species (Martins et al., 2022). Despite fish communities having returned to their overall structure eight months after drying events, not all species have fully recovered. Following the drying events, 17 species experienced a decrease in abundance; among these, seven species did not fully recover to the abundance levels observed prior to the flow loss, even two years after the drought disturbances (Martins et al., 2022).

All biological communities are subject to changes over time (Collins 2000, Magurran et al. 2010). Therefore, it becomes crucial to discern the proportion of these changes caused by natural fluctuations (e.g., temporal changes in environmental conditions or mortality and recruitment processes) and how much of these changes are because of extreme events, which can significantly alter the structure of biological communities. This discernment becomes increasingly urgent in a world with an increase in the frequency and magnitude of extreme events. In this sense, the utilization of temporal β -diversity metrics, which quantify changes in species composition within sites over time, can aid in these efforts to understand how communities are affected by these events (Legendre 2019, Magurran et al. 2019).

Temporal β -diversity can be divided into two components (Baselga, 2010): temporal species turnover, where some species disappear and new species emerge in the community; it is as if the community is renewing itself, with a change in its species composition; and temporal nestedness, which occurs when samples with a lower number of species are, in fact, subsets of samples with greater species richness.

Studies with Amazonian fish assemblages point to habitat connectivity as a fundamental factor in temporal beta diversity patterns at short time scales (seasonal/two months) (Bogotá-Gregory et al., 2023). Rivers and floodplains, systems with greater connectivity, show a higher rate of species turnover than shield and terra-firme streams, regardless of the species richness in these environments. Although the role of temporal nestedness in shaping temporal β -diversity patterns is not yet fully established, the results indicate low values of temporal nestedness in both large river systems (rivers and floodplains) and small streams (shield and terra-firme) (Bogotá-Gregory et al., 2023).

Here, we investigate the effects of extreme drought events on the temporal variation of turnover and nestedness patterns of fish metacommunities in small headwater streams

of the Amazon. From sampling events carried out over 11 years (2012-2023), in a stream system that has perennial water bodies and streams that have suffered from flow loss, we asked: How do temporal changes in species composition promoted by flow loss affect the components of β -diversity temporal? Initially, we postulate that temporal β -diversity will be dominated by turnover over nestedness. Furthermore, we hypothesize that temporal β -diversity of fish communities would be higher in streams that have suffered from flow loss. This is because the loss of flow is responsible for driving a higher rate of temporal species renewal in communities, thereby promoting higher turnover values in these systems.

Methods

Study area

The studied streams are in the region of Volta Grande do Xingu, Brazilian Eastern Amazon (Fig. 1). The region's climate is transitional between “Am” (humid equatorial) and “Af” (hot and humid tropical, with a short dry season and well-defined seasonality) in the Köppen classification (Peel et al., 2007). The average rainfall in the region is 1963.5 mm, mostly concentrated between December and May, with a dry season from June to November (Santos et al., 2016). The average air temperature is 26°C (Ghilardi Jr & Camargo, 2009)

Sampling

Our dataset consists of 262 samples gathered from 23 streams across two sampling cycles (**Fig. 1-2**; Table S1). Eight sites were perennial, eight sites experienced flow loss once, and seven sites experienced two or more flow loss events. The initial cycle spanned from 2012 to 2014, with five sampling events taking place in the rainy season (January-May) and seven in the dry season (July-November). The subsequent cycle featured three sampling events during the dry period (July) in the years 2021, 2022, and 2023 (**Fig. S1**).

Drying prevented sampling at some sites during certain sampling events, particularly at the end of the dry period in 2012, when 15 streams dried out completely or were reduced to disconnected pools. Subsequently, four locations dried out again at the end of the drought in 2013, and seven locations at the end of the drought in 2014. Thus, our database has eight streams that are considered perennial, eight streams dried out completely or were reduced to disconnected pools just once; three streams loss of flow twice, and four streams suffered from the loss of flow three times.

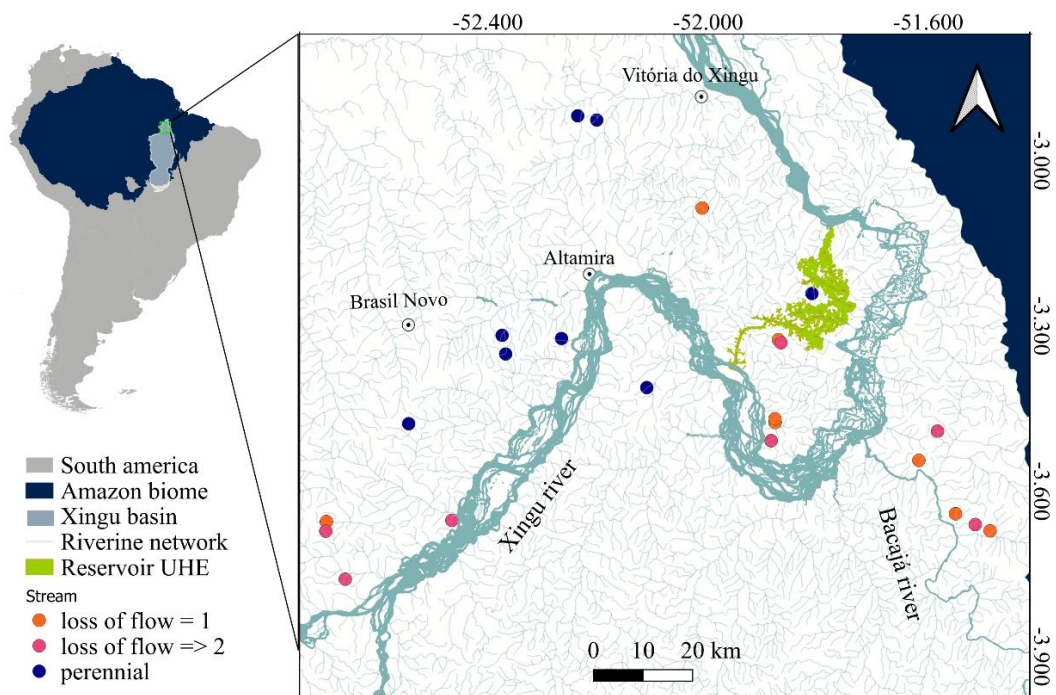


Fig. 1 Geographical locations of sampled stream sites in the region of Volta Grande do Xingu, state of Pará, Brazilian Eastern Amazon. The construction of the reservoir

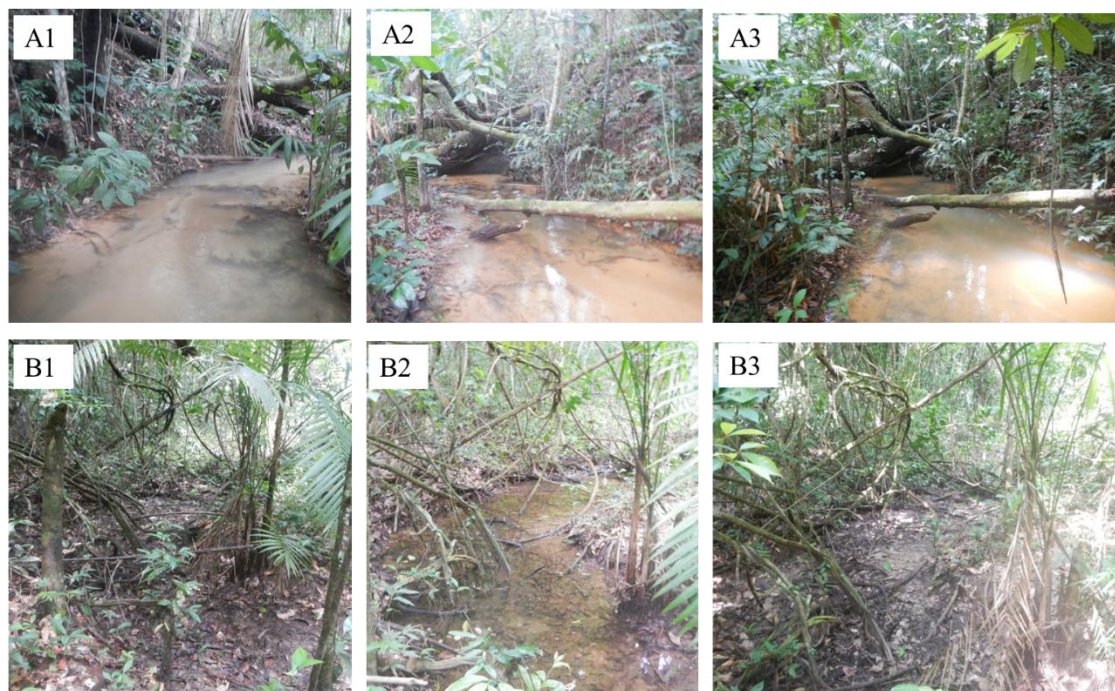


Fig 1 Examples of sampled streams. Images A1-A3 show the same stream at different times, representing streams with more than one flow loss event (photos taken in: A1 - January 2014; A2 - July 2014; b - October 2014). Images B1-B3 depict a perennial stream (photos taken in: B1 - January 2014; B2 - July 2014; B3 - October 2014).

Collection of both the fish and measurement of the physical-chemical features followed the protocol established by Mendonça et al. (2005). We measured local environmental conditions at each stream site (50-meter-long stretch), including channel width, depth, and substrate composition. For each stream and sampling event, these conditions were represented by the averages of measurements taken at six equidistant points along the sampling stretch. The recorded environmental variables included average channel width (m), depth (m), and the relative composition of the substrate (m), categorized based on the frequency of nine types: clay, sand, logs (wood with a diameter greater than 10 cm), leaf litter (composed of leaves and small branches), fine particulate organic matter, roots (primarily fine roots from riparian vegetation), aquatic plants, rocks,

and gravel. Additionally, water conductivity (mS/cm), pH, and water temperature (°C) were measured.

After environmental characterization, fishes were caught using seine nets, and sieves. Captured fish were euthanized with eugenol, fixed in 10% formalin solution, and then preserved in 70% alcohol. Fish collection was conducted under a valid federal permit (IBAMA permit #02001.001848/2006- 75). Voucher specimens are deposited in the INPA Fish Collection (INPA-ICT058292 to INPA-ICT058698).

Data Analyses

To assess the effect of drought events on temporal β -diversity and its components (turnover and nestedness), we divided the streams into three groups according to the hydrological state: perennial streams (perennial: 8), streams with the loss of flow once (loss of flow = > 2: 8), and streams with two or more flow loss events (loss of flow = 1: 7). The efficiency of our sampling effort was then evaluated for each stream, as well as for each hydrological state group, using sample-based rarefaction and the Chao1 species estimator (Chao 1984). The rarefaction curves and Chao 1 estimates were calculated using the ‘*iNEXT*’ (Hsieh et al. 2016) and ‘*vegan*’ (Oksanen et al. 2020) packages, respectively.

Temporal β -diversity partitioning

To analyze temporal β -diversity, we calculated the overall β -diversity, as well as its turnover and nestedness components, for each stream. This involved comparing consecutive sampling periods in chronological order (i.e. time 1–2, 2–3, 3–4 ... 14–15). We used the Jaccard dissimilarity index based on presence/absence data and the `beta.temp` function from the `betapart` package (Baselga & Orme, 2012) to perform these calculations.

Null modeling

To account for the potential influence of local (alpha) diversity on β -diversity and to assess the significance of observed β -diversity patterns, we employed null models (Chase & Myers, 2011; Kraft et al., 2011). To ensure that the null communities generated were ecologically realistic, we developed specific null models for each location, preventing the formation of impossible species combinations (Huttunen et al., 2017). For each stream, we created a matrix with species abundance values (columns) for each sampling event (rows). This matrix was then randomized 1000 times using the `permatfull` function from the `vegan` package (Oksanen et al. 2020). This function employs a quasi-swap algorithm, which shuffles the species matrix while preserving row sums (original species abundances) and column frequencies. For each randomized matrix, we calculated temporal β -diversity, turnover, and nestedness components between adjacent sampling events, following the same procedure used for the original data.

To determine the influence of random versus non-random processes on temporal β -diversity patterns, we calculated the standardized effect size (SES). This metric quantifies the difference between the observed value and the mean of the null distribution, divided by the standard deviation of the null distribution (Chase et al., 2011; Kraft et al., 2011). This allows us to assess the degree to which observed patterns deviate from random expectations

Predictors: the environmental variability, connectivity, and catchment slope

For each sampling site we calculated the environmental variability (EV) (Pereira et al., 2023) between adjacent sampling times in chronological sequence (i.e. time 1–2, 2–3, 3–4 ... 15–16). The environmental variability (EV) was calculated using the standardized Euclidean distance applied to the environmental data over standardized and centralized, previously the environmental variables (except pH) were transformed into $\log(\log x + 1)$.

The average watershed slope (%) was estimated using a digital elevation model derived from the Shuttle Radar Topography Mission (SRTM), available on the EarthExplorer website (<http://earthexplorer.usgs.gov/>). Data processing was conducted using QGIS software (QGIS Development Team, 2021). To analyze stream connectivity, four variables were considered: stream segment link magnitude (Link)(Shreve, 1966), downstream link (D-link) (Osborne & Wiley, 1992), drainage network extension (EDN) (Martins et al., 2024), and distance to the main river (DMS) (Martins et al., 2024). These connectivity variables were calculated in QGIS based on hydrological maps previously developed by Venticinque et al. (2016). Additional methodological details can be found in (Martins et al., 2024; Ribeiro-Martins et al., 2024).

Statistical modelling

For the observed values of temporal β -diversity, turnover component, and for their respective standardized effect size (SES), we built mixed linear models (LMMs) using the *lmer* function from the ‘lme4’ package. For the nestedness component we used linear models. For this, we used the *lm* function. The LMMs were developed considering the hydrological state and its interactions with other predictor variables as fixed factors of the models. These variables include the time between sampling events, slope catchment, stream link magnitude (Link), downstream link (D-link), extension of the drainage network (EDN), and distance from the mainstream (DMS), and the environmental variability (EV). The sampling sites were included as a random effect due to replication between sampling events. The subjacent comparisons over time (1-2, 2-3) were also inserted to control the comparisons between perennial systems and the group of streams that suffered from loss of flow. For the linear model, the sampling sites, and the subjacent comparisons over time (1-2, 2-3) were used as fixed factors. The values of turnover and nestedness were compared through t-test paired within each group according to the

hydrological state. In addition, we used either the Wilcoxon rank-sum test or one-sample t-tests to evaluate whether the mean SES values were different from zero.

Results

We identified 30416 fishes, distributed 106 species (Table S2) (streams perennial 73 species, streams loss of flow = 1: 68 species, and loss of flow = > 2: 74 species). The rarefaction curves approached the asymptote in the three groups of streams (**Fig. 3**). The species richness was 88.8% of the Chao1 richness estimate for the set of perennial streams (obs= 73, est= 82.2), 98.9% for the streams that suffered from the loss of flow only once (obs= 68, est= 68.8); and 77.9% for the streams that suffered from the loss of flow more than once (obs= 74, est= 95).

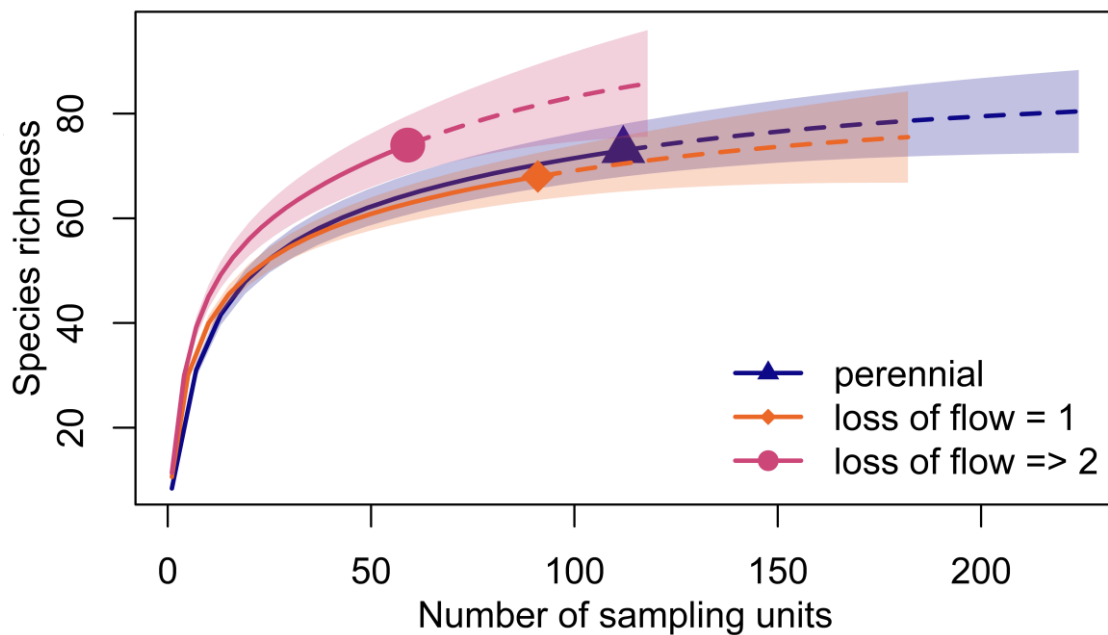


Fig. 2 Extrapolation from species accumulation curves for samples (solid lines) and extrapolated samples (dashed lines) for the fish assemblages of streams in the region of Volta Grande do Xingu, Eastern Amazon of Brazil. The bar error represents the 95% confidence interval. The blue triangle on the blue line represents the observed samples

for perennial streams. The orange diamond represents the streams with a loss of flow once at the end of the 2012 dry, and purple circles for streams with loss of flow $\Rightarrow$ 2.

Regardless of the hydrologic state, the temporal β -diversity was primarily influenced by species turnover, with nestedness playing a minor role (paired t-test: loss of flow $\Rightarrow$ 2: $t = 7.3$, $df = 51$, $P < 0.001$; loss of flow = 1: $t = 5.3$, $df = 82$ $P < 0.001$; perennial: $t = 2.67$, $df = 103$, $P = 0.008$) (**Fig. 4**).

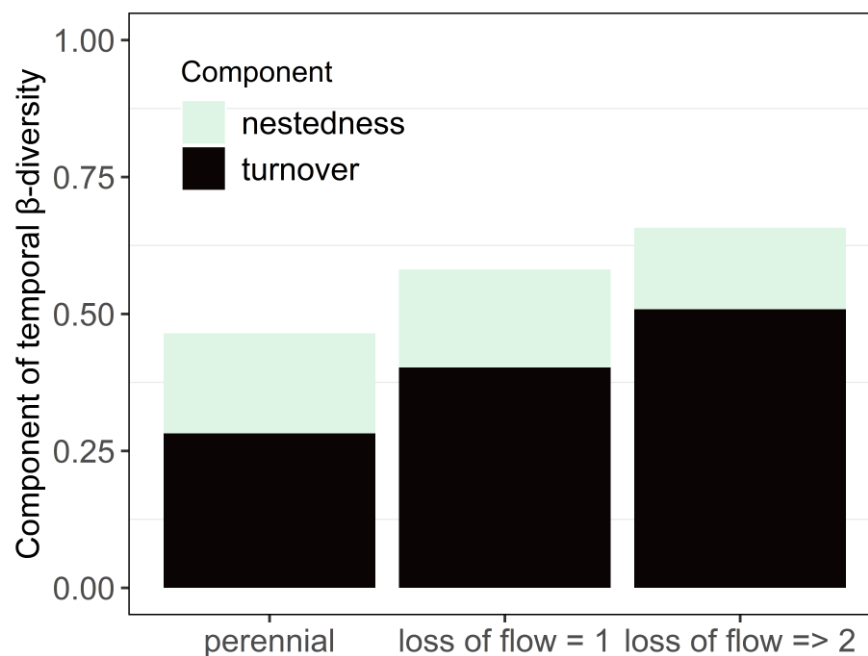


Fig. 4 Contribution of turnover and nestedness to the total temporal β -diversity for the fish assembly of streams in the region of Volta Grande do Xingu Eastern Amazon of Brazil. Left perennial streams, center streams with the loss of flow once, and right streams with loss of flow $\Rightarrow$ 2.

The temporal β -diversity and the observed species turnover over time were notably higher in streams that experienced a loss of flow. The most effective LMMs models only considered the hydrological state (perennial, dried once, or dried multiple times) as a fixed

variable (**Table 1 and Table S3**). For β -diversity, the post hoc comparisons showed significant differences between perennial stream systems and streams with a loss of flow > 2 ($p = 0.001$). However, no differences were detected between perennial and loss of flow $= 1$ ($p = 0.060$), and between loss of flow $= 1$ and loss of flow > 2 ($p = 0.058$) (**Fig. 5a**). For temporal species turnover, the post hoc comparisons showed significant differences between perennial stream systems and streams with a loss of flow > 2 ($p = 0.002$) and between loss of flow $= 1$ and loss of flow > 2 ($p = 0.006$). However, no differences were detected between perennial and loss of flow $= 1$ ($p = 0.150$) (**Fig. 5b**). No significant differences in the temporal nestedness β -deviations were detected between stream types, as the best selected model only had the intercept (**Table 1 and Fig. 5c**).

For all hydrological states, the temporal β -diversity and the species turnover on average were different from the null model (significantly different from zero; Table S4). For the values of nestedness, the results found were not different from random expectations (Table s*). The LMMs models built for the standardized effect size (SES) captured the same fixed (hydrological state) variables from the observed temporal β -diversity and species turnover models (**Fig. 6 and Table 1**).

Table 3 Results from the model selection for general linear models (according to the Akaike information criterion) evaluating the effect of the hydrological state and its interactions with time between sampling events, slope catchment, stream link magnitude (Link), downstream link (D-link), extension of the drainage network (EDN), and distance from the mainstream (DMS), and the environmental variability (EV) as explanatory variables on temporal β -diversity and its components, turnover and nestedness, and for on standard effect size (SES) values of temporal β -diversity and its components, turnover and nestedness

Model	Variables retained in the best model	<i>p</i>	Pseudo-<i>r</i>²
Beta	hydrological state	<0.001	0.30
Turnover	hydrological state	<0.001	0.28
Nestedness	-	-	-
SES Beta	hydrological state	0.004	0.24
SES Turnover	hydrological state	<0.001	0.19
SES Nestedness	-	-	-

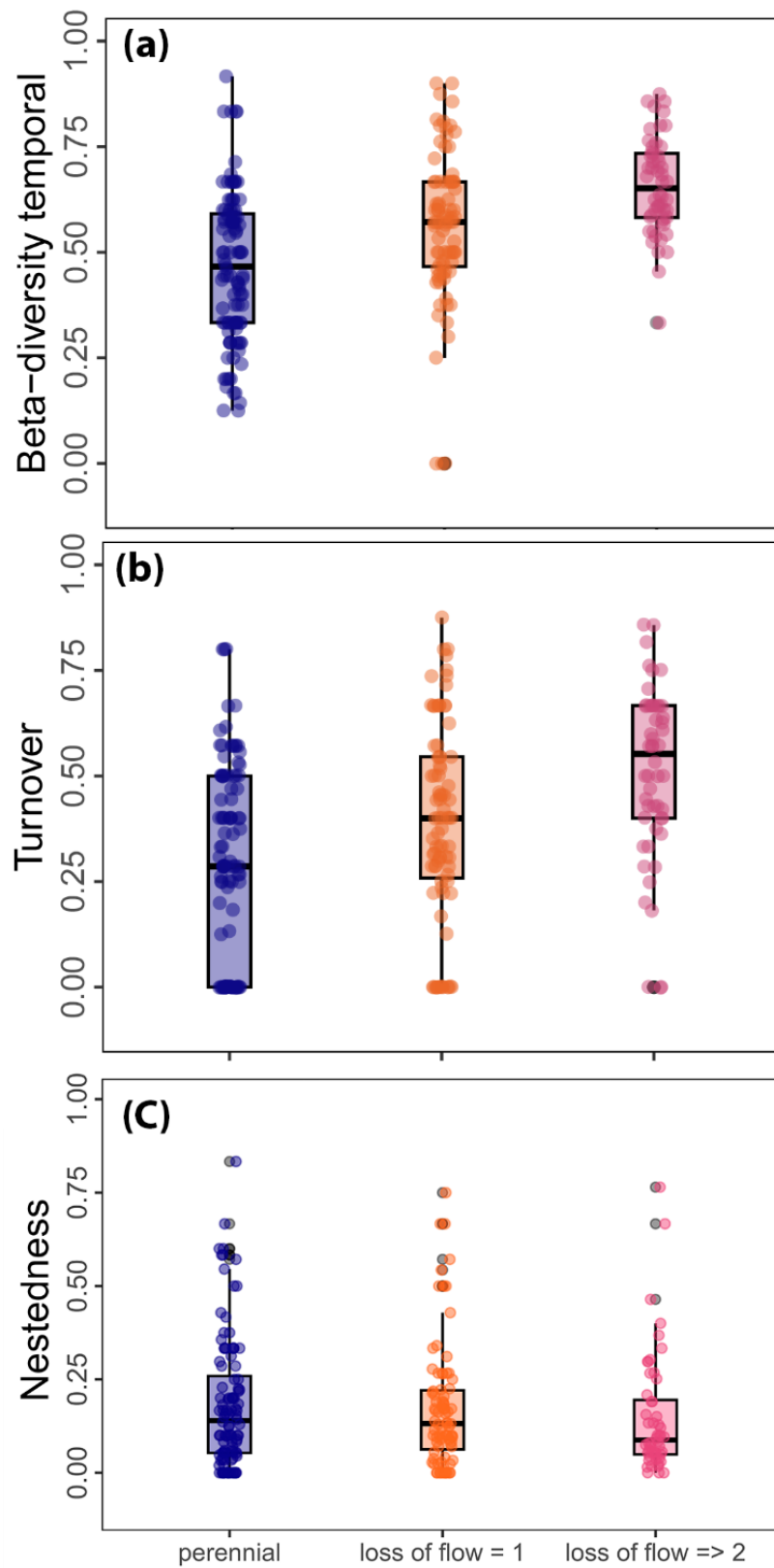


Fig. 3 Comparisons of observed temporal β -diversity (a), species turnover (b) and nestedness (c) with sites divided by hydrological state.

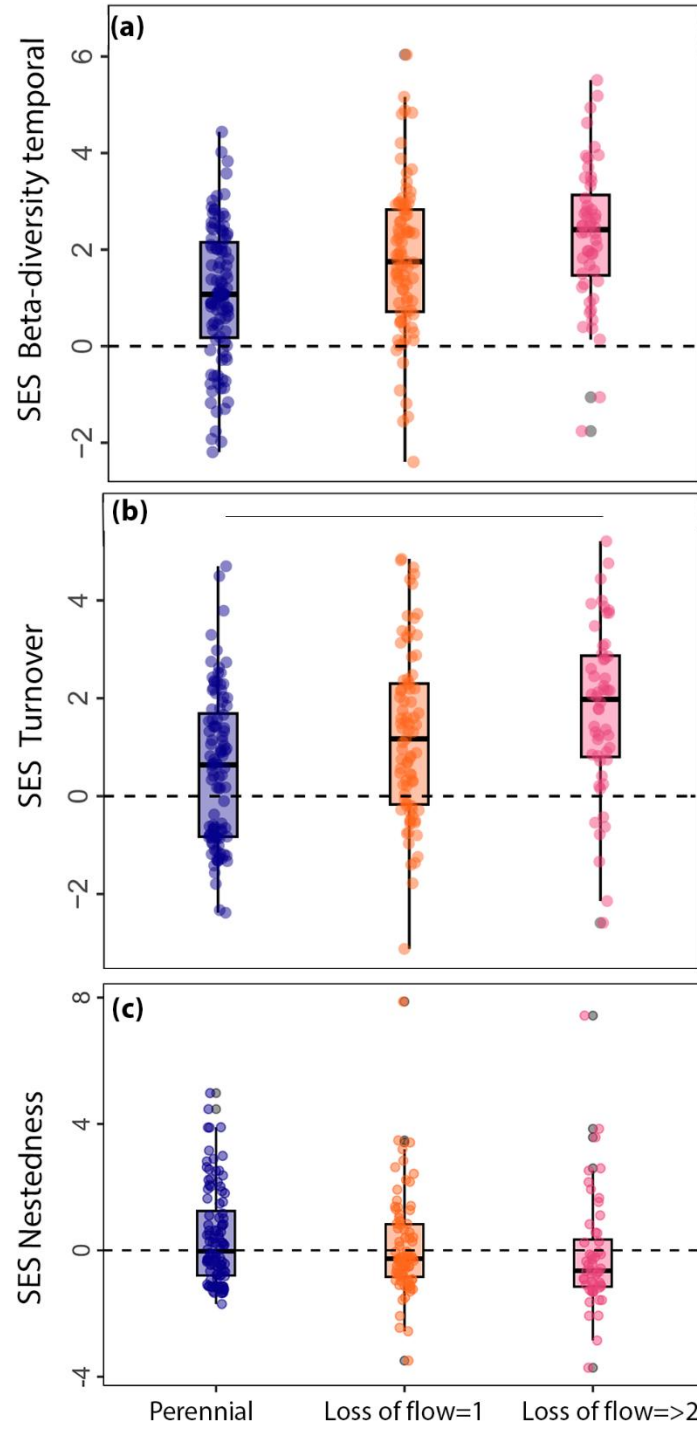


Fig. 4 Comparisons of standard effect size (SES) values of temporal β -diversity (a), species turnover (b) and nestedness (c) with sites divided by hydrological state.

Discussion

All biological communities experience changes over time (Collins 2000, Magurran et al. 2010). But to what extent are these changes natural? And what are the impacts of extreme events on these changes? Here, studying fish assemblages in small Amazonian streams over 11 years, we found that extreme drought events drive temporal β -diversity in these communities. Consistent with our hypotheses, the streams that were affected by flow loss exhibited greater temporal β -diversity compared to the perennial streams. This difference was primarily driven by the temporal species turnover component, highlighting a pattern of species replacement rather than nested subset dynamics in these assemblages (Baselga, 2010). Notably, the severity of extreme drought events further affected temporal β -diversity, with streams experiencing multiple drying events exhibiting higher values of temporal β -diversity and species turnover.

Extreme events alter species turnover rates depending on the environment, the group of organisms, and the type of event, mainly by affecting colonization and migration rates of communities after disturbances (Leibold & Chase, 2018; Magoulick et al., 2021; Saito et al., 2021). Drought events in lotic systems lead to habitat reduction and fragmentation for aquatic organisms, increased water temperature, decreased oxygen levels, and changes in water chemistry (Lake, 2003; 2011); which can lead to mortality of fish and other aquatic organisms, especially those that lack adaptations to withstand low-flow conditions. Furthermore, longitudinal connectivity is disrupted, isolating reaches and altering species composition and abundance (Datry et al., 2014; Lake, 2003). Recovery after drought depends on the presence of refuges, propagule availability, and species dispersal capacity (Lake, 2011; Magoulick & Kobza, 2003). For the studied assemblages, the higher values of temporal species turnover in systems that experienced flow loss should be linked to losses of individuals generated by the drought disturbance

and subsequent recolonization (Martins et al., 2022). After flow loss, these systems underwent a reorganization in community structure, with changes in the presence and absence of new species, as well as alterations in the abundance of species present in local communities. However, this new reorganization detected three months after flow loss was no longer found eight months after flow loss, with the overall community structure returning to the values detected before flow loss (Martins et al., 2022). The studied region of the Xingu River basin exhibits regular precipitation patterns (Santos et al., 2016), which should enable the presence of numerous perennial reaches (even in periods of lower precipitation) that served as a source of propagules for the return of species to sites that suffered from flow loss (Martins et al., 2022; Matthaei et al., 2000; Sedell et al., 1990). Moreover, the pools that remained during the drying process may have served as a source of recolonization for some species (Fernandes et al., 2015; Lake, 2011; Martins et al., 2022).

It is not well-defined to what extent nestedness becomes the main driver of temporal β -diversity. During a typical hydrological cycle, where any fluctuations in diversity patterns should be considered natural, the temporal beta-diversity patterns of the Amazonian ichthyofauna, both in floodplain systems (high hydrological connectivity) and streams (shield and terra-firme streams; low hydrological connectivity) were driven mainly by turnover, and not by changes in nestedness (Bogotá-Gregory et al., 2023). Extreme events were detected as responsible for nestedness being the main component of temporal β -diversity in intermittent streams subject to extreme drying, while turnover is the main component of temporal β -diversity in streams with higher predictability in seasonality (Datry et al 2016; Perkin et al). This contribution of nestedness to temporal β -diversity in these systems should be directly linked to the loss of species promoted by these periodic drying events (Lake, 2011). The recolonization process following flow loss

events, driven by propagule availability (Martins et al., 2022; Matthaei et al., 2000; Sedell et al., 1990), appears to be the main mechanism behind the low contribution of nestedness and the increased turnover in fish communities of terra-firme streams in the Amazon. The local extirpation of fish populations in streams affected by flow loss, followed by recolonization from perennial systems, resulted in a pattern of species replacement, rather than the formation of nested subsets. Furthermore, the use of null models allows us to isolate the effect of species richness (Chase & Myers, 2011; Kraft et al., 2011), highlighting that turnover values are related to post-drought recolonization processes (Martins et al., 2022).

The positive relationship between β -diversity and environmental variability is well established in spatial analyses (Heino et al., 2015; Zbinden et al., 2022). However, in the temporal context, this pattern is less consistent. For example, the temporal β -diversity of zooplankton communities increased with increasing environmental variability between high and low water periods in the Araguaia River floodplain (Pereira et al., 2023). However, Lopes et al., 2019, found opposing results in a tropical reservoir. The lack of relationship between temporal β -diversity and environmental variability in our analyses may be related to drying events, as hydrological variation is the dominant force affecting stream communities, overriding other abiotic and biotic factors (Magoulick & Kobza, 2003). Our results indicate that hydrological variation is indeed a mechanism that overrides other factors. At the spatial scale, both local environmental variables (e.g., stream depth and width) and landscape variables (e.g., catchment slope), as well as the connectivity of water bodies in the drainage network, are responsible for the patterns of functional and phylogenetic diversity and uniqueness in fish assemblages in the Volta Grande do Xingu region (Martins et al., 2024). These factors are also responsible for the distribution pattern of fish species throughout this same region (Martins et al., 2023).

The temporal dynamics of biological communities have become a central focus for ecologists, as evidenced by Czeplédi et al. (2022), who identified 307 scientific articles on the topic in freshwater fish assemblages. However, this synthesis revealed a crucial gap: the scarcity of research in the Neotropical region (less than 10%), which harbors the world's most diverse freshwater fish fauna, with about 5,750 species (Dagosta & Pinna, 2019). This deficiency is particularly worrisome given the predictions of intensification of extreme climatic events, driven by global climate change (IPCC, 2023; Prudhomme et al., 2014).

Understanding how biological communities respond to such events is essential to predict the consequences of these changes on their structure (Donohue et al., 2016). Long-term studies in regions with a history of environmental and climatic fluctuations, such as North America and Europe, show that fish communities in these regions are resistant and resilient to disturbances such as extreme droughts and floods, exhibiting transient fluctuations in the structure (e.g., species composition and richness) of the fish assemblages analyzed (Franssen et al., 2011; Magalhães et al., 2007; Matthews & Marsh-Matthews, 2003, 2016). In contrast, the Amazonian fish fauna has been shown to be more sensitive to changes in environmental conditions (Borba et al., 2021; Freitas et al., 2013; Martins et al., 2022; Röpke et al., 2017). The severe drought of 2005, for example, caused lasting changes in the fish community within a floodplain lake in Central Amazonia (Röpke et al., 2017). Before the drought, the fish community was more diverse, with a greater variety of species. However, the drought led to a decrease in species diversity, with some species disappearing completely. Additionally, the relative abundance of different species changed, with some species becoming more common and others less common (Röpke et al., 2017). In addition to these sudden changes, gradual changes in the fish communities of terra firme streams in Central Amazonia have also been observed

(Borba et al., 2021). Over an 18-year period, increased rainfall and a greater number of storms in Central Amazonia altered stream beds, shifting from leaf-litter dominated substrates to sand-dominated substrates. These changes led to shifts in the types of fish found in these streams, favoring species adapted to sandy bottoms and open waters, such as those with streamlined bodies and well-developed fins. They negatively impact species that prefer litter-rich substrates and slower-moving waters (Borba et al., 2021).

Conclusions

Our study focused on how extreme drought events affect the temporal β -diversity in fish assemblages in small headwater streams of the Amazon. From samples collected over 11 years (2012-2023), we found that in both perennial streams and those that suffered from flow loss, the species turnover component is the main driver of the temporal β -diversity of these assemblages. However, despite turnover being the main component in all scenarios, drought events intensify this mechanism. The recolonization process after disturbances generates a new species composition where there is no nestedness in these assemblages, but rather a replacement process. Our results provide important baseline information that demonstrates that drought intensify the mechanisms that influence the temporal stability of these assemblages. This is a worrying situation given the scenarios of intensifying droughts in the Brazilian Eastern Amazon (Sorribas et al., 2016), which may put at risk a considerable portion of the basin's ichthyofauna.

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Supplementary Material

Table S1. Summary of fish collection activities and environmental variables in each stream during the 23 sampling campaigns conducted from 2012 to 2014, and in 2021, 2022, and 2023, in the region of Volta Grande do Xingu, Pará state, Brazilian Eastern Amazon. 1 = Sampling successfully performed; 2 = Streams that dried up or with no flow (isolated ponds); 3 = Very high-water volume (no conditions to perform standardized sampling); 4 = No access to the site (trail closed by vegetation or blocked road); 5 = Collection point had not yet been implemented; 6 = Collection point is no longer inventoried.* = sampling was carried out, however, no specimen was collected.

Stream	Hydrological state	2012				2013				2014				2021	2022	2023
		Rainy season		Dry season		Rainy season		Dry season		Rainy season		Dry season		Jun/Jul	Jul	Jun/Jul
		Mar/Apr	June	Sept/ Oct	Nov	Jan	Apr	Jul	Oct	Jan/Feb	Apr	Ju	Oct			
ST06	perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ST07	perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ST08	perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ST10	perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ST14	perennial	1	4	1	1	1	1	4	1	1	4	1	1	1	1	1
ST19	perennial	1	1	1	1	1	1	1	1	1	1	1	1	6	6	6
ST20	perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ST22	perennial	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ST03	loss of flow once	1	4	2	2	1	1	1	1	1	1	1	1	1	1	1
ST12	loss of flow once	1	1	2	2	1	3	1	1	1	1	1	1	1	1	1
ST13	loss of flow once	1	1	1	2	1	3	1	1	1	3	1	1	1	1	1
ST17	loss of flow once	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1
ST21	loss of flow once	1	1	1*	2	1	1	1	1	1	1	1	1*	1	1	1
ST23	loss of flow once	4	1	1	2	1	1	1	1	1	1	1	1	6	6	6
ST25	loss of flow once	4	1	2	2	1	4	1	1	1	4	1	1	1	1	1
ST26	loss of flow once	4	1	2	2	1	4	1	1	1	4	1	1	1	1	1
ST01	flow loss =>2	1	1	2	2	1	1	1	2	2	1	1	2	1	1	5
ST02	flow loss =>2	1	1	2	2	1	1	1	1	1	1	1	2	1	5	1
ST05	flow loss =>2	1	2	2	2	3	1	1	2	2	4	2	2	5	5	1

ST11	flow loss =>2	1	1	2	2	2	1	1	2	2	1	1	2	1	1	1
ST16	flow loss =>2	1	4	2	2	1	1	1	2	1	4	1	2	1	1	1
ST28	flow loss =>2	4	1	2	2	2	1	1	1	1	1	1	2	1	1	1
ST29	flow loss =>2	4	1	2	2	1*	4	3	1	1	4	1	2	1	1	1

Table S2. List of fish species sampled in 23 streams in the region of Volta Grande do Xingu, state of Pará, Brazilian Eastern Amazon. Occurrence refers to the total number of streams where the species were found.

Order	Family	Species	perennial	loss of flow =1	loss of flow => 2
Characiformes	Acestrorhynchidae	<i>Acestrorhynchus falcatus</i> (Bloch 1794)	x	x	x
Characiformes	Anostomidae	<i>Leporinus</i> cf. <i>granti</i> Eigenmann, 1912	x		
Characiformes	Anostomidae	<i>Leporinus friderici</i> (Bloch, 1794)	x	x	x
Characiformes	Anostomidae	<i>Leporinus torrenticola</i> Birindelli, Teixeira & Britski 2016		x	x
Characiformes	Bryconidae	<i>Brycon falcatus</i> Müller & Troschel, 1844	x	x	x
Characiformes	Characidae	<i>Astyanax anterior</i> Eigenmann 1908		x	x
Characiformes	Characidae	<i>Astyanax elachylepis</i> Bertaco & Lucinda 2005	x	x	x
Characiformes	Characidae	<i>Astyanax</i> aff. <i>bimaculatus</i> (Linnaeus, 1758)	x	x	x
Characiformes	Characidae	<i>Creagrutus</i> cf. <i>ignotus</i> Vari & Harold 2001		x	x
Characiformes	Characidae	<i>Ctenobrycon spilurus</i> (Valenciennes, 1850)		x	
Characiformes	Characidae	<i>Hemigrammus bellottii</i> (Steindachner, 1882)	x		
Characiformes	Characidae	<i>Hemigrammus ocellifer</i> (Steindachner, 1882)		x	
Characiformes	Characidae	<i>Hemigrammus</i> sp. "prata"			x
Characiformes	Characidae	<i>Hemigrammus</i> sp. "collettii"	x	x	x
Characiformes	Characidae	<i>Hyphessobrycon copelandi</i> Durbin, 1908		x	x
Characiformes	Characidae	<i>Hyphessobrycon heterorhabdus</i> (Ulrey, 1894)	x		
Characiformes	Characidae	<i>Hyphessobrycon juruna</i> Faria, Lima & Bastos 2018			x
Characiformes	Characidae	<i>Hyphessobrycon</i> sp. "faixa negra"		x	
Characiformes	Characidae	<i>Jupiaba apenima</i> Zanata 1997		x	
Characiformes	Characidae	<i>Jupiaba polylepis</i> (Günther, 1864)	x	x	x
Characiformes	Characidae	<i>Knodus</i> aff. <i>savannensis</i>	x	x	x

Characiformes	Characidae	<i>Moenkhausia celibela</i> Marinho & Langeani, 2010	x	x	x
Characiformes	Characidae	<i>Moenkhausia comma</i> Eigenmann, 1908	x	x	x
Characiformes	Characidae	<i>Moenkhausia oligolepis</i> (Günther, 1864)	x	x	x
Characiformes	Characidae	<i>Moenkhausia pirauba</i> Zanata, Birindelli & Moreira, 2010	x	x	x
Characiformes	Characidae	<i>Phenacogaster</i> aff. <i>calverti</i> (Fowler 1941)			x
Characiformes	Characidae	<i>Phenacogaster</i> aff. <i>napoatilis</i> Lucena & Malabarba 2010	x	x	x
Characiformes	Characidae	<i>Poptella brevispina</i> Reis, 1989	x	x	x
Characiformes	Characidae	<i>Poptella fortispina</i> Garcia-Ayala & Benine 2023		x	x
Characiformes	Characidae	<i>Serrapinnus tocantinensis</i> Malabarba & Jerep 2014	x	x	
Characiformes	Characidae	<i>Tetragonopterus argenteus</i> Cuvier, 1816	x		
Characiformes	Characidae	<i>Tetragonopterus chalceus</i> Spix & Agassiz, 1829			x
Characiformes	Characidae	<i>Thayeria boehlkei</i> Weitzman 1957	x		x
Characiformes	Crenuchidae	<i>Characidium</i> aff. <i>zebra</i> Eigenmann, 1909	x	x	x
Characiformes	Crenuchidae	<i>Characidium</i> sp. "faixa"			x
Characiformes	Crenuchidae	<i>Melanocharacidium dispilomma</i> Buckup 1993			x
Characiformes	Crenuchidae	<i>Microcharacidium</i> aff. <i>weitzmani</i> Buckup, 1993	x		
Characiformes	Curimatidae	<i>Cyphocharax gouldingi</i> Vari, 1992	x		x
Characiformes	Curimatidae	<i>Steindachnerina amazonica</i> (Steindachner 1911)			x
Characiformes	Erythrinidae	<i>Erythrinus erythrinus</i> (Bloch & Schneider, 1801)	x	x	x
Characiformes	Erythrinidae	<i>Hoplerythrinus unitaeniatus</i> (Spix & Agassiz, 1829)	x	x	x
Characiformes	Erythrinidae	<i>Hoplias curupira</i> Oyakawa & Mattox, 2009	x		
Characiformes	Erythrinidae	<i>Hoplias malabaricus</i> (Bloch, 1794)	x	x	x
Characiformes	Hemiodontidae	<i>Bivibranchia velox</i> (Eigenmann & Myers, 1927)			x
Characiformes	Iguanodectidae	<i>Bryconops</i> aff. <i>caudomaculatus</i> (Günther, 1864)	x		
Characiformes	Iguanodectidae	<i>Bryconops</i> aff. <i>magoi</i> Chernoff & Machado-Allison, 2005			x
Characiformes	Iguanodectidae	<i>Bryconops affinis</i> (Günther, 1864)	x	x	x
Characiformes	Iguanodectidae	<i>Bryconops melanurus</i> (Bloch, 1794)	x		
Characiformes	Iguanodectidae	<i>Iguanodectes rachovii</i> Regan, 1912	x		
Characiformes	Lebiasinidae	<i>Copella arnoldi</i> (Regan, 1912)	x	x	x
Characiformes	Lebiasinidae	<i>Pyrrhulina capim</i> Vieira & Netto-Ferreira 2019	x	x	

Characiformes	Prochilodontidae	<i>Prochilodus nigricans</i> Spix & Agassiz, 1829	x		
Characiformes	Serrasalminidae	<i>Myloplus rubripinnis</i> (Müller & Troschel, 1844)	x		x
Cichliformes	Cichlidae	<i>Acaronia nassa</i> (Heckel 1840)	x		
Cichliformes	Cichlidae	<i>Aequidens tetramerus</i> (Heckel 1840)	x	x	x
Cichliformes	Cichlidae	<i>Apistogramma gephyra</i> Kullander, 1980	x		
Cichliformes	Cichlidae	<i>Apistogramma</i> sp.		x	x
Cichliformes	Cichlidae	<i>Apistogramma</i> sp. tracejado	x	x	
Cichliformes	Cichlidae	<i>Apistogramma</i> sp. vielfleck		x	
Cichliformes	Cichlidae	<i>Crenicichla</i> gr. <i>saxatilis</i> (Linnaeus, 1758)	x	x	x
Cichliformes	Cichlidae	<i>Hypselecara temporalis</i> (Günther 1862)	x		
Cichliformes	Cichlidae	<i>Retroculus xinguensis</i> Gosse 1971		x	x
Cichliformes	Cichlidae	<i>Satanoperca</i> aff. <i>jurupari</i> (Heckel, 1840)	x		
Cyprinodontiformes	Poeciliidae	<i>Pamphorichthys araguaiensis</i> Costa 1991	x	x	x
Cyprinodontiformes	Rivulidae	<i>Anablepsoides xinguensis</i> (Costa, 2010)	x	x	x
Cyprinodontiformes	Rivulidae	<i>Melanorivulus rubroreticulatus</i> Costa, Amorim & Bragança 2014	x		
Gymnotiformes	Gymnotidae	<i>Gymnotus carapo</i> Linnaeus, 1758	x	x	x
Gymnotiformes	Gymnotidae	<i>Gymnotus coropinae</i> Hoedeman, 1962	x		x
Gymnotiformes	Hypopomidae	<i>Brachyhypopomus</i> aff. <i>regani</i> Crampton, de Santana, Waddell & Lovejoy 2017		x	x
Gymnotiformes	Hypopomidae	<i>Brachyhypopomus beebei</i> (Schultz, 1944)		x	x
Gymnotiformes	Hypopomidae	<i>Brachyhypopomus brevirostris</i> (Steindachner 1868)	x		
Gymnotiformes	Hypopomidae	<i>Brachyhypopomus</i> aff. <i>beebei</i>			x
Gymnotiformes	Hypopomidae	<i>Microsternarchus</i> aff. <i>bilineatus</i> Fernández-Yépez, 1968	x	x	
Gymnotiformes	Rhamphichthyidae	<i>Gymnorhamphichthys rondoni</i> (Miranda Ribeiro, 1920)	x	x	x
Gymnotiformes	Rhamphichthyidae	<i>Hypopygus lepturus</i> Hoedeman 1962	x		
Gymnotiformes	Rhamphichthyidae	<i>Steatogenys duidae</i> (La Monte, 1929)	x		
Gymnotiformes	Sternopygidae	<i>Eigenmannia</i> aff. <i>trilineata</i> López & Castello, 1966	x	x	x
Gymnotiformes	Sternopygidae	<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	x	x	x
Myliobatiformes	Potamotrygonidae	<i>Potamotrygon</i> aff. <i>orbignyi</i> (Castelnau, 1855)			x

Siluriformes	Auchenipteridae	<i>Auchenipterichthys punctatus</i> (Valenciennes, 1840)	x		
Siluriformes	Auchenipteridae	<i>Tatia</i> aff. <i>gyrina</i> (Eigenmann & Allen, 1942)		x	x
Siluriformes	Auchenipteridae	<i>Tatia intermedia</i> (Steindachner, 1877)	x	x	x
Siluriformes	Callichthyidae	<i>Callichthys callichthys</i> (Linnaeus, 1758)	x	x	x
Siluriformes	Callichthyidae	<i>Corydoras</i> cf. <i>aeneus</i> (Gill, 1858)	x	x	x
Siluriformes	Callichthyidae	<i>Corydoras</i> sp. "c87"			x
Siluriformes	Callichthyidae	<i>Megalechis picta</i> (Müller & Troschel, 1849)		x	x
Siluriformes	Cetopsidae	<i>Cetopsidium orientale</i> (Vari, Ferraris & Keith 2003)			x
Siluriformes	Cetopsidae	<i>Denticetopsis epa</i> Vari, Ferraris & de Pinna 2005	x	x	
Siluriformes	Cetopsidae	<i>Helogenes marmoratus</i> Günther, 1863	x	x	x
Siluriformes	Heptapteridae	<i>Imparfinis</i> aff. <i>hasemani</i> Steindachner, 1917	x	x	x
Siluriformes	Heptapteridae	<i>Mastiglanis asopos</i> Bockmann 1994	x	x	
Siluriformes	Heptapteridae	<i>Phenacorhamdia</i> sp.	x	x	x
Siluriformes	Heptapteridae	<i>Pimelodella</i> sp. "faixa grossa"	x	x	x
Siluriformes	Heptapteridae	<i>Rhamdia quelen</i> (Quoy & Gaimard 1824)	x	x	x
Siluriformes	Loricariidae	<i>Ancistrus luzia</i> Neuhaus, Britto, Birindelli & Sousa 2022	x		
Siluriformes	Loricariidae	<i>Ancistrus</i> sp. "L100"	x		
Siluriformes	Loricariidae	<i>Ancistrus</i> sp. "bola"	x	x	x
Siluriformes	Loricariidae	<i>Curculionichthys</i> sp. "alto"		x	x
Siluriformes	Loricariidae	<i>Hypostomus</i> aff. <i>plecostomus</i> (Linnaeus, 1758)	x	x	x
Siluriformes	Loricariidae	<i>Hypostomus hemiochliodon</i> Kner, 1854		x	x
Siluriformes	Loricariidae	<i>Otocinclus</i> cf. <i>hasemani</i> Steindachner 1915		x	x
Siluriformes	Loricariidae	<i>Rineloricaria lanceolata</i> (Günther, 1868)	x	x	x
Siluriformes	Loricariidae	<i>Rineloricaria</i> sp.	x	x	x
Siluriformes	Pseudopimelodidae	<i>Batrochoglanis villosus</i> (Eigenmann 1912)		x	x
Siluriformes	Trichomycteridae	<i>Ituglanis</i> aff. <i>amazonicus</i> (Steindachner 1882)	x	x	x
Synbranchiformes	Synbranchidae	<i>Synbranchus</i> aff. <i>madeira</i> Rosen & Rumney, 1972	x	x	x

Table S3 Results from the model selection for general linear models (according to the Akaike information criterion) evaluating the effect of the hydrological state and its interactions with time between sampling events, slope catchment, stream link magnitude (Link), downstream link (D-link), extension of the drainage network (EDN), and distance from the mainstream (DMS), and the environmental variability (EV) as explanatory variables on temporal β -diversity and its components, turnover and nestedness, and for on standard effect size (SES) values of temporal β -diversity and its components, turnover and nestedness. Models excluding outliers.

Model	Variables retained in the best model	<i>p</i>	Pseudo- <i>r</i> ²
Outliers removed			
Beta	hydrological state	<0.001	0.40
Turnover	hydrological state	<0.001	0.28
Nestedness	-	-	-
Outliers removed			
SES Beta	hydrological state	0.004	0.24
SES Turnover	hydrological state	<0.001	0.19
SES Nestedness	-	-	-

Table S4 One-sample t-test and Wilcoxon rank-sum test were used to assess whether SES indices differed from zero in each hydrological state. The test statistic (t or W), degrees of freedom (for t-tests only), and p-values are reported.

Index	Test	Hydrological state	mean	t	W	p-value
SES Beta	One-sample t-tests	perennial	1.08	7.82	-	<0.001
SES Beta	One-sample t-tests	loss of flow once	1.78	10.37	-	<0.001
SES Beta	One-sample t-tests	flow loss =>2	2.31	11.395	-	<0.001
SES Turnover	Wilcoxon rank-sum	perennial	0.56	-	3739	0.001
SES Turnover	One-sample t-tests	loss of flow once	1.24	6.61	-	<0.001
SES Turnover	One-sample t-tests	flow loss =>2	1.76	7.42	-	<0.001
SES Nestedness	Wilcoxon rank-sum	perennial	0.4	-	3150	0.173
SES Nestedness	Wilcoxon rank-sum	loss of flow once	0.09	-	1631	0.612
SES Nestedness	Wilcoxon rank-sum	flow loss =>2	-0.14	-	498	0.082

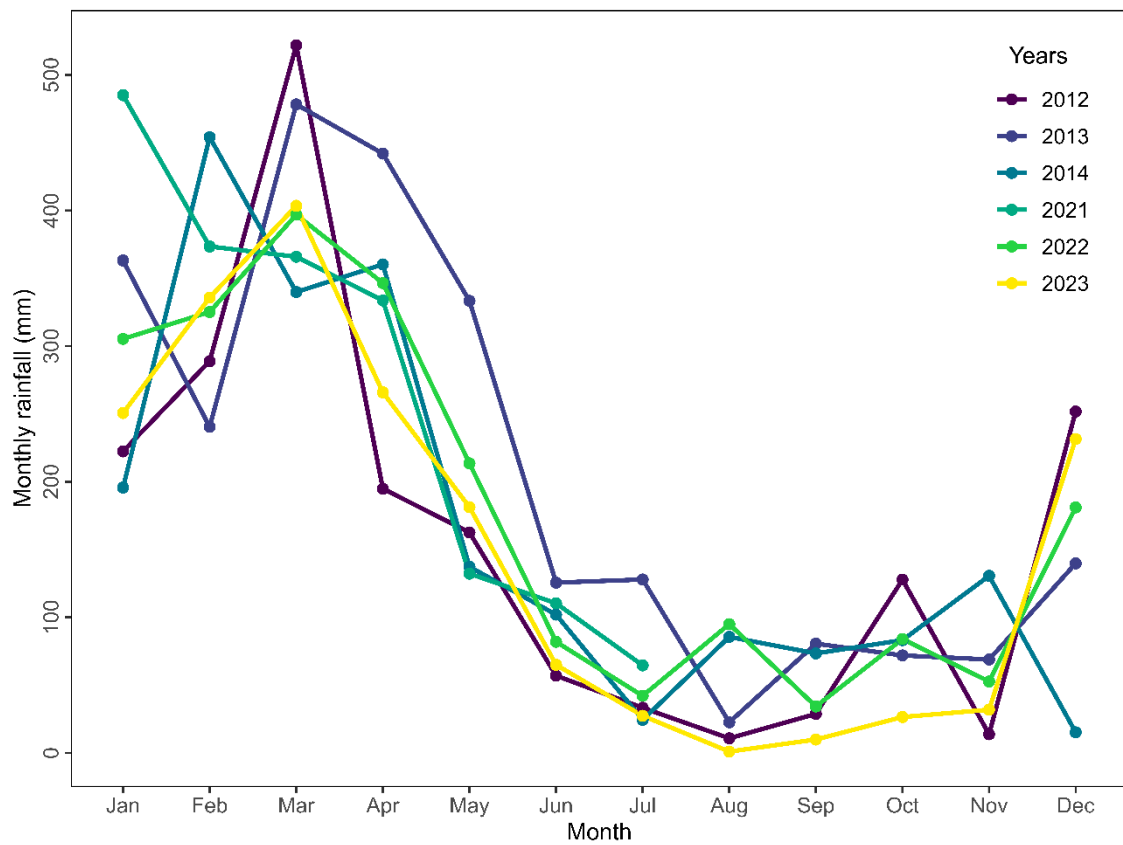


Figure S1 Monthly rainfall (in mm) for the collection years 2012-2014 and 2021-2023, recorded at the meteorological station in the municipality of Altamira, Pará, Brazil. The year 2021 has no station records for the dry season (July-December)

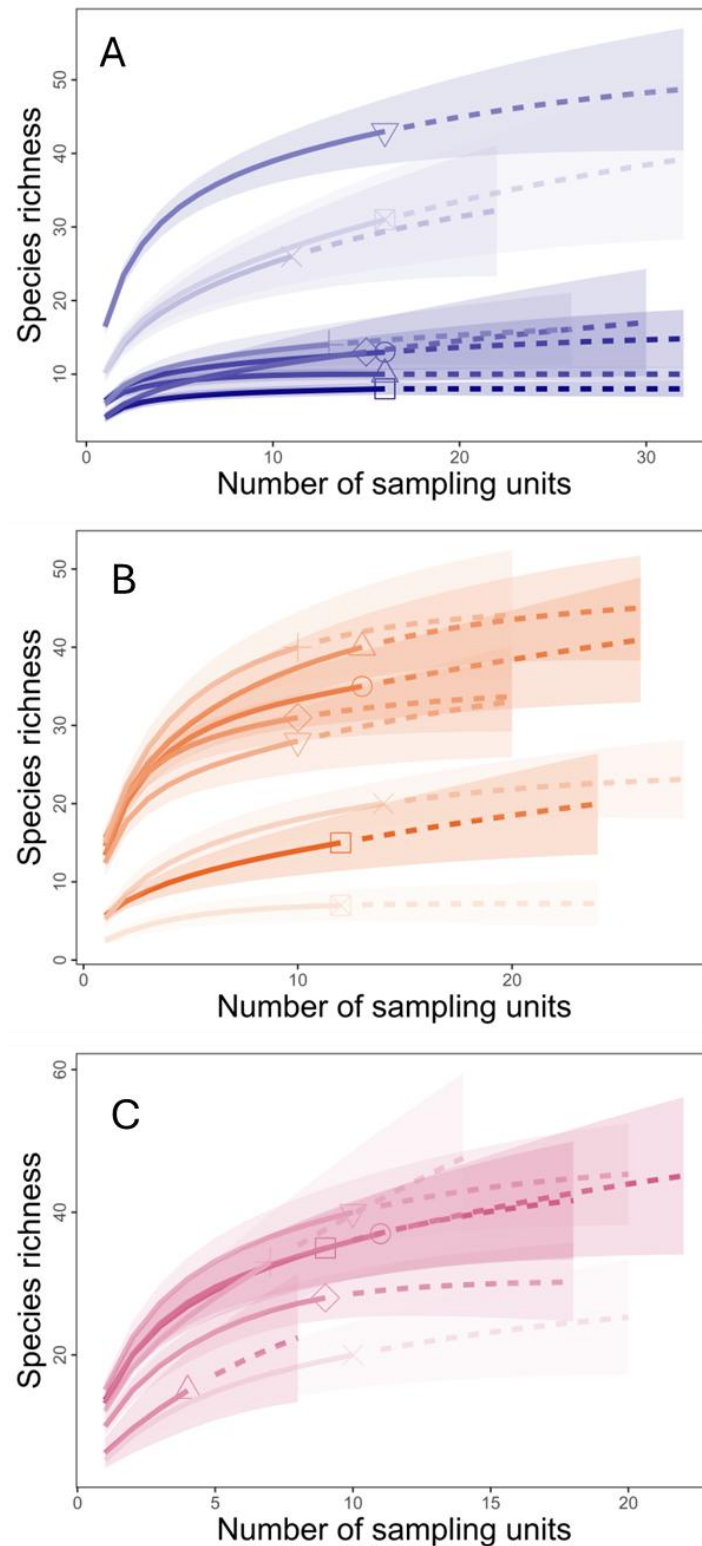


Figure 5. Extrapolation from species accumulation curves for samples (solid lines) and extrapolated samples (dashed lines) for the fish the fish assemblages of streams in the region of Volta Grande do Xingu, Eastern Amazon of Brazil. The bar error represents the 95% confidence interval. (A) Perennial streams, (B) streams with a loss of flow once at the end of the 2012 dry, and (C) streams with loss of flow $\Rightarrow$ 2.

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

Nesta Tese, investiguei os efeitos de múltiplos fatores, que incluem, a influência de interações interespecíficas, da conectividade dos corpos hídricos na rede de drenagem, de variáveis ambientais em múltiplas escalas, de variáveis espaciais, temporais, incluindo eventos de secas extremas sobre a fauna de peixes em pequenos riachos da Amazônia Central. Para isso, utilizei um extenso banco de dados de peixes e de características ambientais locais de 30 pequenos riachos de terra-firme da Volta Grande do Xingu, coletados ao longo de 11 anos (2012-2023). Além dos dados coletados em campo, construí conjuntos de dados que capturam a estrutura funcional e filogenética das assembleias estudadas. Também calculei variáveis espaciais e ambientais na escala da bacia como variáveis preditoras. Utilizando diferentes abordagens ecológicas e análises estatísticas avançadas, investiguei a contribuição desse conjunto de fatores nos padrões de múltiplas facetas (taxonômica, funcional e filogenética) de assembleias de peixes de riachos da Amazônia. Especificamente:

No primeiro capítulo, utilizamos a estrutura de metacomunidade proposta por THOMPSON *et al.* (2020), que reorganizaram o conceito da teoria de metacomunidade buscando unir teorias sobre coexistência em escala local (por exemplo, CHESSON, 2000; GAUSE, 1932; LOTKA, 1922; SHOEMAKER; MELBOURNE, 2016; VOLTERRA, 1926), com processos ligados à heterogeneidade ambiental e dispersão (THOMPSON *et al.*, 2020). Assim, analisamos os efeitos de fatores ambientais (em múltiplas escalas espaciais), da configuração da rede de drenagem, autocorrelação espacial e interações interespecíficas na dinâmica de metacomunidades de peixes de riachos de terra-firme na Amazônia. Nossos resultados são consistentes com estudos anteriores que detectaram o efeito das condições ambientais e da limitação de dispersão como principais preditores da dinâmica de metacomunidades de peixes de riachos (MIRANDA; MAZZONI, 2009; PALHETA *et al.*, 2021). Além disso, destacamos a importância de analisar preditores em múltiplas escalas, por exemplo, disponibilidade local de substrato e declividade da bacia hidrográfica nos padrões de distribuição das espécies nas assembleias locais. Em adição destacamos a importância de inserir aspectos da estrutura espacial da bacia de drenagem, que caracterize a conectividade dos trechos de amostragem na rede hidrográfica. Inicialmente, utilizamos o rio principal (Xingu ou Bacajá) como barreira e calculamos toda a extensão (km) da rede de drenagem disponível para as assembleias dos trechos amostrados até o rio principal. Os resultados mostram que quanto maior a rede de drenagem, menor a abundância da maioria das espécies

(14 de 15) que responderam a essa variável. É de suma importância destacar que nesse capítulo, nossas inferências se baseiam em uma análise focada nas espécies mais comuns. Espécies raras, registradas em menos de três dos 30 riachos amostrados, foram removidas do nosso modelo para evitar uma superestimação da importância das covariáveis. Assim, é possível que as espécies raras possam responder de maneira oposta a essa variável, isso porque os pequenos riachos da amazônica têm muitas espécies de pequeno porte com distribuições restritas e capacidade limitada de migração (CASTRO, 1999; MENDONÇA; MAGNUSSON; ZUANON, 2005). Fatores bióticos sempre são destacados como um dos filtros finais na dinâmica de organização das comunidades biológicas (VELLEND, 2016). Nossos resultados demonstram que a nível de metacomunidade, para os peixes de pequenos riachos de cabeceiras as interações interespecíficas têm pouca influência na distribuição e dinâmica nesses ecossistemas. Nossos resultados reforçam as conclusões iniciais de PERES-NETO, 2004, de que a elevada heterogeneidade dos riachos neotropicais pode diminuir a relevância das interações bióticas na dinâmica e na distribuição das comunidades de peixes nesses ambientes.

No segundo capítulo encontramos que os padrões de diversidade funcional e filogenética, assim como a singularidade filogenética de peixes de riachos de cabeceiras da Amazônia, são explicados pelas condições ambientais locais e pela conectividade dos riachos na rede de drenagem. Também vimos que a singularidade funcional é exclusivamente associada às condições ambientais. Assim, destacamos que a diversidade e a singularidade ecológica analisadas a partir das facetas funcionais e filogenéticas dos peixes desses sistemas são fortemente estruturados por processos baseados em nicho. Em adição, encontramos conjuntos de preditores distintos para os padrões de diversidade e singularidade entre as estações chuvosa e seca, enfatizando a importância de considerar os efeitos da sazonalidade para uma melhor compreensão do processo de organização da ictiofauna dos riachos de terra firme amazônicos (ESPÍRITO-SANTO *et al.*, 2009; ESPÍRITO-SANTO; ZUANON, 2017). Durante o período chuvoso, a diversidade funcional e a diversidade filogenética foram explicadas pela conectividade da rede de drenagem e no período de estiagem pelas condições ambientais locais. Já a singularidade funcional, durante o período chuvoso foi explicada por variáveis ambientais locais e durante a estiagem pela declividade da bacia de drenagem. Por fim, a singularidade filogenética foi explicada conjuntamente pelas condições ambientais locais e pela conectividade em ambos os períodos. Além disso, verificamos que ao longo do trecho estudado (Volta Grande do Xingu), a ictiofauna mantém uma consistência na estrutura funcional e filogenética, pois, espacialmente, diferente da faceta taxonômica, a estrutura

espacial não contribuiu para os padrões encontrados, indicando que existe uma história funcional e filogenética estreitamente compartilhada entre os riachos estudados, provavelmente devido aos efeitos da estabilidade climática e ambiental vivenciada pela ictiofauna amazônica ao longo do tempo evolutivo (OBERDORFF *et al.*, 2019; PERES *et al.*, 2010).

No terceiro capítulo nos concentramos em como eventos de secas extremas afetam a diversidade beta temporal em comunidades de peixes de pequenos riachos de cabeceira na Amazônia. Para isso, utilizamos dados coletados ao longo de 11 anos (2012-2023) em riachos perenes e riachos que sofreram perda de fluxo (seca completa ou formação de poças isoladas) durante o período de estudo. Tanto em riachos perenes quanto naqueles afetados por perda de fluxo, o componente de substituição de espécies foi identificado como o principal impulsionador da diversidade beta temporal; indicando que a mudança na composição das comunidades de peixes ao longo do tempo é devido à entrada e saída de espécies, e não à formação de subconjuntos aninhados de espécies. Embora a substituição seja o componente dominante em ambos os tipos de riachos, os eventos de seca amplificam esse mecanismo. A perda de fluxo e a subsequente recolonização levam a uma reorganização da comunidade, com novas espécies entrando e outras desaparecendo, resultando em uma maior substituição temporal. A recolonização pós-seca, parece estar relacionada à disponibilidade de propágulos de áreas adjacentes e à persistência de algumas espécies em poças remanescentes (BOGAN; BOERSMA; LYTLE, 2015; FERNANDES; PENHA; ZUANON, 2015; LANCASTER, 2000; MATTHAEI; ARBUCKLE; TOWNSEND, 2000). Os resultados indicam que a ictiofauna de riachos amazônicos é sensível a eventos extremos de seca, com a diversidade beta temporal sendo significativamente afetada. Essa vulnerabilidade é preocupante, considerando os cenários de intensificação das secas na Amazônia Oriental brasileira (SORRIBAS *et al.*, 2016).

Para finalizar esta Tese deixo aqui algumas perspectivas para futuros estudos com base nos achados descritos ao longo deste documento:

- Abordamos no primeiro capítulo a estrutura geral da metacomunidade de peixes, para isso espécies com ocorrência em menos de três riachos foram retiradas das análises para evitar uma superestimação da importância das covariáveis. Assim, é importante que trabalhos futuros verifiquem qual o efeito das espécies raras na dinâmica dessas metacomunidades.
- Ainda em uma perspectiva de metacomunidades, focamos em um padrão geral ao longo da tese. Nesse sentido, a modelagem hierárquica conjunta de distribuição de espécies utilizada no primeiro capítulo mostrou uma variação muito grande dos preditores individuais

de cada espécie, trabalhos futuros poderão avançar nessas respostas individuais das espécies e em como essas respostas contribuem para a dinâmica dessas assembleias.

- Assim como as espécies individualmente foram negligenciadas ao longo da Tese, a contribuição dos locais individualmente também ficou em segundo plano. Assim, trabalhos futuros poderão se beneficiar da estrutura analítica proposta por LEIBOLD et al. (2022), que reconhecem a necessidade de analisar a heterogeneidade dentro das metacomunidades, focando nas contribuições específicas das espécies e dos locais para os padrões gerais.

- No segundo capítulo, focamos em índices de diversidade, utilizando a diversidade e singularidade funcional e filogenética. Trabalhos futuros, que abordem a estrutura filogenética, utilizando por exemplo, as Coordenadas Principais da Estrutura Filogenética (PCPS) serão úteis na compreensão de como a composição de clados responde aos gradientes ambientais e temporais. Assim como análises que busquem identificar como esses gradientes filtram os traços funcionais que utilizamos na construção dos índices.

- Será crucial também entender como os eventos de secas extremas afetam a diversidade funcional e filogenética. Aqui focamos apenas na faceta taxonômica. Funcionalmente, os eventos de secas podem levar a uma diminuição da originalidade funcional e a um aumento da redundância funcional desses locais.

- Utilizamos algumas variáveis de conectividade, que mostraram ser um importante preditor. Trabalhos futuros podem focar na importância da conectividade e de possíveis refúgios na capacidade de recolonização após eventos de secas.

- Também se torna de suma importância aprimorar a identificação de áreas suscetíveis à perda de fluxo e aprimorar as previsões sobre os impactos das mudanças climáticas nos ecossistemas aquáticos da Amazônia.

- Na área de estudo (Volta Grande do Xingu) está situado um dos maiores empreendimentos hidroelétricos do mundo, a Usina Hidrelétrica de Belo Monte, construída entre 2011-2015. Nosso conjunto de dados do primeiro e segundo capítulo (30 sites) foram coletados entre 2012-2013 durante o processo de construção do empreendimento. O terceiro capítulo, utiliza dados coletados a cada três meses entre 2012 e 2014 e anualmente durante o período de estiagem entre 2021 e 2023. Ao longo dos capítulos não abordamos possíveis efeitos da construção do empreendimento nas comunidades de peixes de riachos. No terceiro capítulo, utilizamos o conjunto de dados mais abrangentes, que inclui dados (2012-2014) dos primeiros anos de construção do empreendimento e dados (2021 2022 e 2023) seis anos após o barramento total do rio (2015). As análises do terceiro capítulo comparam ao longo do

tempo para cada riacho as amostragens adjacentes em sequência cronológica (ou seja, tempo 1-2, 2-3, 3-4 ... 15-16). Investigações futuras podem analisar de maneira direta se as assembleias de peixes dos riachos mais próximos aos sistemas de barramento apresentam alguma mudança na dinâmica espaço-temporal usando como controle os riachos que não estão diretamente ligados às modificações causadas pelo empreendimento.

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ANEXOS

Artigos que compõem a Tese

1. Martins, A. R., Bastos, D. A., Sousa, L. M., Giarrizzo, T., Vieira, T. B., & Hepp, L. U. (2024). Metacommunity organisation of Amazonian stream fish assemblages: The importance of spatial and environmental factors. *Ecology of Freshwater Fish*, 33, e12750. <https://doi.org/10.1111/eff.12750>

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ORIGINAL ARTICLE

Ecology of
FRESHWATER FISH | WILEY

Metacommunity organisation of Amazonian stream fish assemblages: The importance of spatial and environmental factors

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Abstract

Metacommunity theory seeks to explain how local and regional processes contribute to the organisation of biological communities. Recent conceptual frameworks of this theory indicate that the dynamics of populations and communities are jointly established by dispersal, species responses to environmental conditions and biotic interactions dependent on species density. Here, we use hierarchical joint species distribution modelling to verify the effects of environmental factors (at multiple spatial scales), drainage network configuration, spatial autocorrelation and interspecific interactions on the structure of fish assemblages in *terra-firme* streams in the Eastern Brazilian Amazon. Thirty streams were sampled in two field surveys, and 89 species were collected in total. Our results confirm the effects of limited dispersal, environmental conditions (at multiple scales) and the configuration of the drainage network on the dynamics of these assemblages. Furthermore, our results suggest that interspecific interactions are less relevant for the structuring of fish metacommunities in small Amazonian headwater streams. Abiotic factors like drainage networks and environmental heterogeneity were better predictors of species distributions than co-occurrence patterns with potential competitors or predators.

KEYWORDS

community ecology, freshwater fish, ichthyofauna, interspecific interactions, metacommunity, riverine network

2. Ribeiro-Martins, A., Bastos, D. A., Sousa, L. M., Giarrizzo, T., Milesi, S. V., & Hepp, L. U. (2024). The role of the environment and connectivity on multiple facets of local fish diversity in tropical headwater streams. *Freshwater Biology*, 69, 1376–1389. <https://doi.org/10.1111/fwb.14312>

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ORIGINAL ARTICLE

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The role of the environment and connectivity on multiple facets of local fish diversity in tropical headwater streams

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Abstract

1. The identification of multiple facets of biodiversity (e.g., phylogenetic and functional) can help to understand how evolutionary and ecological mechanisms shape the assembly of biological communities.
2. Here, we employed multiple regressions and variance partitions to investigate the effects of environmental conditions, connectivity and space on aspects of the functional and phylogenetic facets of fish fauna in tropical headwater streams of the Xingu River basin, in Eastern Amazonia.
3. We found that the functional and phylogenetic diversities of fish communities are related to local environmental conditions and stream connectivity in the drainage network, with marked differences occurring between the rainy and dry periods. Furthermore, we discovered that functional uniqueness was influenced mainly by environmental factors, whereas phylogenetic uniqueness had a more complex relationship with the influence of local environmental factors and connectivity.
4. Our findings indicate that the fish assemblages of small headwater streams of the Xingu River basin share a close phylogenetic history. This is probably because of the climatic and environmental stability experienced by Amazonian ichthyofauna over evolutionary time.
5. Our findings emphasise the role of niche-based processes in shaping the unique functional composition of fish assemblages in headwater streams, and highlight the importance of environmental heterogeneity in maintaining the ecological integrity of these freshwater ecosystems.

KEYWORDS

Amazon ichthyofauna, ecological uniqueness, functional diversity, phylogenetic diversity, spatial variation

Artigos publicados durante o processo de doutoramento que não compõem a tese (julho/2020-dezembro/2024)

1. Lubich CCF, Martins AR, Freitas CEC, Hurd LE, Siqueira-Souza FK (2021) A candiru, *Paracanthopoma* sp. (Siluriformes: Trichomycteridae), associated with a thorny catfish, *Doras phlyzakion* (Siluriformes: Doradidae), in a tributary of the middle Rio Negro, Brazilian Amazon. *Acta Ichthyologica et Piscatoria* 51(3): 241–244. <https://doi.org/10.3897/aiep.51.64324>
2. Martins, A. R, Bastos, D. A., Sousa, L. M., Giarrizzo, T., Vieira, T. B., & Zuanon, J. (2022). Intense droughts affect temporal stability of Amazonian stream fish assemblages. *Freshwater Biology*, 67, 1656-1667. <https://doi.org/10.1111/fw.b.13970>

Aceitos para publicação durante o processo de doutoramento que não compõem a tese (julho/2020-dezembro/2024)

3. Nascimento, A. C. L.; **Ribeiro-Martins, A**; dias-silva, K.; Juem, L.; Mortati, A. F.; Oliveira Junior, J. M. B. Species and Site Contributions to Odonata adult assemblage uniqueness in Brazilian Amazon streams. *Journal of Insect Conservation*, 2025.
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Autorizações



MINISTÉRIO DO MEIO AMBIENTE
INSTITUTO BRASILEIRO DO MEIO AMBIENTE E DOS RECURSOS NATURAIS RENOVÁVEIS
DIRETORIA DE LICENCIAMENTO AMBIENTAL

AUTORIZAÇÃO DE CAPTURA, COLETA E TRANSPORTE DE MATERIAL BIOLÓGICO

PROCESSO IBAMA: 02001.001848/2006-75	AUTORIZAÇÃO: 057/2012	VALIDADE: 31/12/2014
ATIVIDADE: ☐ LEVANTAMENTO ☒ MONITORAMENTO ☐ RESGATE/SALVAMENTO TIPO: ☐ RECURSOS FAUNÍSTICOS ☒ RECURSOS PESQUEIROS		
EMPREENDEDOR: Norte Energia S/A CNPJ: 12.300.288/0001-07 CTF: 5.074.556 ENDEREÇO: SCN Quadra 4 – Bloco B, salas 904 e 1004 Asa Norte – Centro Empresarial VARIG Brasília – DF – CEP: 70.714-900 EMPREENDIMENTO: AHE Belo Monte		
CONSULTORIA RESPONSÁVEL PELA ATIVIDADE: Biotrópica Projetos e Consultoria Ambiental Ltda CNPJ/CPF: 10.766.635/0001-58 CTF: 4.401.547		
COORDENADOR GERAL DA ATIVIDADE: Tommaso Giarrizzo CPF: 526.336.242-00 CTF: 203.065		
DESCRIÇÃO DA ATIVIDADE: Monitoramento da ictiofauna e ictioplâncton durante o período de instalação e operação do Aproveitamento Hidrelétrico de Belo Monte. O monitoramento de ictiofauna será realizado no âmbito do Programa de Monitoramento da Ictiofauna, integrante do Plano Básico Ambiental do AHE Belo Monte. Os métodos de captura autorizados são redes de emalhe com malhas de 2, 4, 7, 10, 12, 15 e 18cm entre nós opostos; espinhéis com anzóis de tamanhos 06/0, 12/0 e 14/0; peneiras; redes de arrasto; coleta manual em mergulho livre; tarrafa com malha de 1,6cm entre nós opostos e altura de 2,7m; puçás; arrasto de fundo; e rede de plâncton com de malha de 300µm.		
PROCEDÊNCIA: Municípios de Altamira, Vitória do Xingu, Senador José Porfírio, Brasil Novo; e Anapu no estado do Pará.		
DESTINAÇÃO DO MATERIAL: Museu Paraense Emílio Goeldi (MCT/MPEG).		
ESTA AUTORIZAÇÃO NÃO PERMITE: 1. CAPTURA/COLETA/TRANSPORTE/SOLTURA DE ESPÉCIES EM ÁREA PARTICULAR SEM O CONSENTIMENTO DO PROPRIETÁRIO; 2. CAPTURA/COLETA/TRANSPORTE/SOLTURA DE ESPÉCIES EM UNIDADES DE CONSERVAÇÃO FEDERAIS, ESTADUAIS, DISTRITAIS OU MUNICIPAIS, SALVO QUANDO ACOMPANHADAS DA ANUÊNCIA DO ÓRGÃO ADMINISTRADOR COMPETENTE; 3. COLETA DE ESPÉCIES LISTADAS NA INSTRUÇÃO NORMATIVA MMA Nº 05/2004, OBSERVADAS AS ALTERAÇÕES DA INSTRUÇÃO NORMATIVA MMA Nº 52/2005, NOS ANEXOS CITES, NA VERSÃO MAIS RECENTE DO LIVRO VERMELHO DA FAUNA BRASILEIRA AMEAÇADA DE EXTINÇÃO, E NO ANEXO DA RESOLUÇÃO COEMA 54/2007; 4. COLETA DE MATERIAL BIOLÓGICO SEM A SUPERVISÃO DE TÉCNICOS LISTADOS NESTA AUTORIZAÇÃO; 5. EXPORTAÇÃO DE MATERIAL BIOLÓGICO; 6. ACESSO AO PATRIMÔNIO GENÉTICO, NOS TERMOS DA REGULAMENTAÇÃO CONSTANTE NA MEDIDA PROVISÓRIA Nº 2.186-16, DE 23 DE AGOSTO DE 2001.		
LOCAL E DATA DE EMISSÃO: 19 MAR 2012	AUTORIDADE EXPEDIDORA (ASSINATURA E CARIMBO): Gisela Damm Foratti Diretora de Licenciamento Ambiental IBAMA	

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PARECER CONSUBSTANCIADO DO CEP

DADOS DO PROJETO DE PESQUISA

Título da Pesquisa: Desenvolvimento de metodologias inovadoras de restauração ecológica com ênfase no enriquecimento nutricional para a fauna do trecho de vazão reduzida da UHE Belo Monte (PA): integrando modelos bioeconômicos à conservação dos ecossistemas amazônicos.

Pesquisador: TOMMASO GIARRIZZO

Área Temática:

Versão: 1

CAAE: 57396222.1.0000.0018

Instituição Proponente: Programa de Pós-graduação em Ecologia Aquática e Pesca

Patrocinador Principal: NORTE ENERGIA S/A

DADOS DO PARECER

Número do Parecer: 5.392.573

Apresentação do Projeto:

Projeto de Pesquisa intitulado "Desenvolvimento de metodologias inovadoras de restauração ecológica com ênfase no enriquecimento nutricional para a fauna do trecho de vazão reduzida da UHE Belo Monte(PA): integrando modelos bioeconômicos à conservação dos ecossistemas amazônicos".

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