

**UNIVERSIDADE FEDERAL DE MINAS GERAIS**

**Instituto de Ciências Biológicas**

**Departamento de Genética, Ecologia e Evolução**

**Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida  
Silvestre**

Carlos Alberto de Sousa Rodrigues Filho

**IMPORTÂNCIA DE PROCESSOS HISTÓRICOS E ECOLÓGICOS PARA  
ESTRUTURAÇÃO FUNCIONAL DE COMUNIDADES DE PEIXES DE  
RIACHOS NEOTROPICAIS**

Belo Horizonte – MG

2022

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ESTRUTURAÇÃO FUNCIONAL DE COMUNIDADES DE PEXIES DE  
RIACHOS NEOTROPICAIS**

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Orientador: Dr. Rafael Pereira  
Leitão

Coorientador: Dr. Fabricio  
Beggiato Baccaro

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**Ata da Defesa de Tese**

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**Carlos Alberto de Sousa Rodrigues Filho**

No dia 21 de março de 2022, às 08:30 horas, por vídeo conferência, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) Carlos Alberto de Sousa Rodrigues Filho, orientando do Professor Rafael Pereira Leitão, intitulada: **“Importância de processos históricos e ecológicos para estruturação funcional de comunidades de peixes de riachos Neotropicais”**. Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) Rafael Pereira Leitão, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Naraiana Loureiro Benone (UEMG), Fabricio Barreto Teresa (UEG), Frederico de Siqueira Neves (UFMG), Fernanda Alves Martins (CIBIO/PORTUGAL) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

- (X) Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;  
( ) Reavaliação da tese com avaliação pelos membros da banca do documento revisado, sem nova defesa, no prazo máximo de 30 dias, sob possibilidade de reprovação;  
( ) Reformulação da tese com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG a ao Regimento do PPG-ECMVS;  
( ) Reprovação

A banca indica esta tese aos Prêmios CAPES e UFMG de teses? (X) SIM ( ) NÃO

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 21 de março de 2022.

Assinaturas dos Membros da Banca Examinadora



Documento assinado eletronicamente por **Naraiana Loureiro Benone, Usuária Externa**, em 25/03/2022, às 09:47, conforme horário oficial de Brasília, com fundamento no art. 5º do [Decreto nº 10.543, de 13 de novembro de 2020](#).



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## Resumo

A história evolutiva e biogeográfica desempenha um importante papel em moldar os padrões diversidade do conjunto regional de espécies (i.e., pool) dentro e entre regiões biogeográficas. Sínteses recentes sugerem que esses eventos definem o pool de espécies por meio de três processos fundamentais: especiação, extinção e dispersão. Por outro lado, processos ecológicos locais (i.e., filtragem ambiental) são reconhecidos por explicar os padrões de estrutura das comunidades locais (e.g., composição e abundância de espécies). Essa ideia tem sido confrontada por estudos empíricos de larga escala, mesmo naqueles que abordam a diversidade funcional, faceta da biodiversidade na qual se espera alta relação com processos ecológicos locais. Possivelmente, em amplas escalas espaciais processos históricos e ecológicos atuam em conjunto para explicar os padrões locais de diversidade biológica. Para testar tal hipótese, utilizamos um banco de dados de peixes de riachos com informações refinadas de condições ambientais, composição e abundância de espécies, bem como informações de atributos ecomorfológicos, tróficos e comportamentais de dois biomas brasileiros: Amazônia e Caatinga. Nossos principais objetivos foram: 1) estimar a importância da história filogenética, fatores espaciais e ambientais em explicar a dinâmica de metacomunidades de peixes de riachos da Caatinga; 2) investigar os mecanismos pelos quais assembleias de peixes de riachos da Amazônia são organizadas (filtragem de habitat e similaridade limitante) e como são influenciados por fatores históricos e ecológicos; e 3) determinar se as diferenças na estrutura funcional do pool de espécies entre Amazônia e Caatinga modulam a importância de condições ambientais dos riachos em prever a estrutura funcional local dos peixes de riachos. Para o primeiro objetivo, utilizamos 27 riachos de cabeceiras da Caatinga distribuídos em três diferentes 'brejos de altitude' e avaliamos como a importância relativa da história filogenética, fatores espaciais e ambientais em explicar as estruturas taxonômicas e funcionais das assembleias. Observamos que a histórica filogenética explica boa parte da variação taxonômica e funcional das metacomunidades de peixes de riachos. Esse resultado já é esperado para a abordagem taxonômica, mas representa um importante achado para a abordagem funcional. Assim, em pequenos riachos de cabeceiras da Caatinga, a história filogenética é capaz de explicar os padrões funcional que presumivelmente seria explicado por fatores ambientais. Para o segundo objetivo, utilizamos 307 riachos distribuídos em 21 sub-bacias de 11 bacias hidrográficas da Amazônia brasileira com diferentes intensidades de processos históricos. Por exemplo, sub-bacias mais ao Oeste apresentam relativa estabilidade histórica, enquanto sub-bacias mais ao Leste foram submersas por água do mar há ~5 Mya, o que possivelmente extinguiu toda a fauna de água doce. Construímos modelos nulos específicos para investigar como as assembleias de peixes são organizadas do pool global de espécies (375 espécies) até as assembleias locais, assumindo um algoritmo de limitação de dispersão e que a atuação da filtragem ambiental e similaridade limitante atuam em diferentes escalas. Encontramos que assembleias de peixes de riachos da Amazônia são regidas predominantemente por similaridade limitante. Em adição, encontramos que os eventos de incursão marinhas do passado em conjunto com condições ambientais dos riachos e tipo de água modulam o sinal da filtragem ambiental e similaridade limitante ao longo de 21 sub-bacias. Assim, concluímos que as consequências de eventos históricos são observadas atualmente nos padrões de montagem de assembleias em peixes de riachos da Amazônia. Finalmente, investigamos se condições ambientais locais (por exemplo, velocidade da correnteza) produzem estrutura funcional semelhante entre 53 riachos da Amazônia e 54 da Caatinga. Encontramos que a estrutura funcional do pool de espécies difere significativamente entre os biomas e que condições locais não explicam as diferenças na estrutura funcional entre os biomas. Esse resultado foi mais bem entendido após a execução de uma técnica de reamostragem paramétrica balanceada que amostra 10 riachos de cada bioma, no qual encontramos que quanto maior a diferença na estrutura funcional do pool de espécies menor a capacidade das condições ambientais em explicar a estrutura funcional das assembleias de peixes entre Amazônia e Caatinga. Acreditamos que esses resultados em conjunto fornecem importantes avanços na ecologia funcional ao longo de largas escalas espaciais, principalmente para ecossistemas tropicais de peixes de riachos.

Palavras-chave: Biogeografia funcional, metacomunidades, montagem de comunidades, peixes de riachos

## Abstract

Evolutionary and biogeographic history play an important role in shaping patterns of regional diversity of species (i.e., species pool) within and between biogeographic regions. Recent syntheses suggest that these events act from three fundamental processes: speciation, extinction, and dispersal. On the other hand, local ecological processes (i.e., habitat filtering) are recognized to explain the patterns of structure of local communities (e.g., species composition and abundance). This idea has been confronted by large-scale empirical studies, even those that address functional diversity, a facet of biodiversity recognized to be strongly related with ecological processes. Possibly, at large spatial scales, historical and ecological processes act together to explain local patterns of biological diversity. To test this hypothesis, we used a fish database from streams with refined information on environmental conditions, species composition and abundance, as well as information on ecomorphological, trophic and behavioral attributes of two Brazilian biomes: Amazon and Caatinga. Our main aim were: 1) to estimate the importance of phylogenetic history, spatial and environmental factors in explaining the dynamics of fish metacommunities from Caatinga streams; 2) investigate the mechanisms by which Amazonian stream fish assemblages are organized (habitat filtering and limiting similarity) and how they are influenced by historical and ecological drivers; and 3) to determine whether differences in the functional structure of the species pool between Amazon and Caatinga can modulate the importance of stream environmental conditions in predicting the local functional structure of stream fish. For the first objective, we used 27 headwater streams of the Caatinga distributed in three different “brejos de altitude” and evaluated the relative importance of phylogenetic history, spatial and environmental factors in explaining the taxonomic and functional structures of the assemblages. We observed that phylogenetic history explains much of the taxonomic and functional variation of stream fish metacommunities. This result is already expected for the taxonomic approach but represents an important finding for the functional approach. Thus, in small headwater streams of the Caatinga, phylogenetic history appears as an important driver of the functional patterns that would presumably be explained by environmental factors. For the second objective, we used 307 streams distributed in 21 sub-basins of 11 hydrographic basins in the Brazilian Amazon with different evolutionary histories. For example, Western sub-basins show relative historical stability, while Eastern sub-basins have submerged by seawater ~5 Mya ago, which possibly eliminated all freshwater fauna. We built specific null models to investigate how fish assemblages are organized from the global pool of species (375 species) to local assemblages, assuming a dispersion limitation algorithm and that the importance of the environmental filtering and the limiting similarity act at different scales. We found that fish assemblages from Amazon streams are predominantly governed by limiting similarity. In addition, we found that past marine incursion events together with stream environmental conditions and water type modulate the environmental filtering signal and limiting similarity across 21 sub-basins. Thus, we conclude that the consequences of historical events are currently observed in the assembly patterns of assemblages in fish from Amazon streams. Finally, we investigated whether local environmental conditions (e.g., water velocity) yield similar functional structure between 53 streams in the Amazon and 54 in the Caatinga. We found that the functional structure of the species pool differs significantly between biomes and that local conditions do not explain the differences in functional structure between biomes. This result was better understood after performing a balanced parametric resampling technique that samples 10 streams from each biome, in which we found that the greater the difference in the functional structure of the species pool, the lower the capacity of environmental conditions to explain the structure. function of fish assemblages between Amazon and Caatinga. We believe that these results together provide important advances in functional ecology over large spatial scales, particularly for tropical stream fish ecosystems.

Keywords: Functional biogeography, metacommunities, community assembly, stream fish

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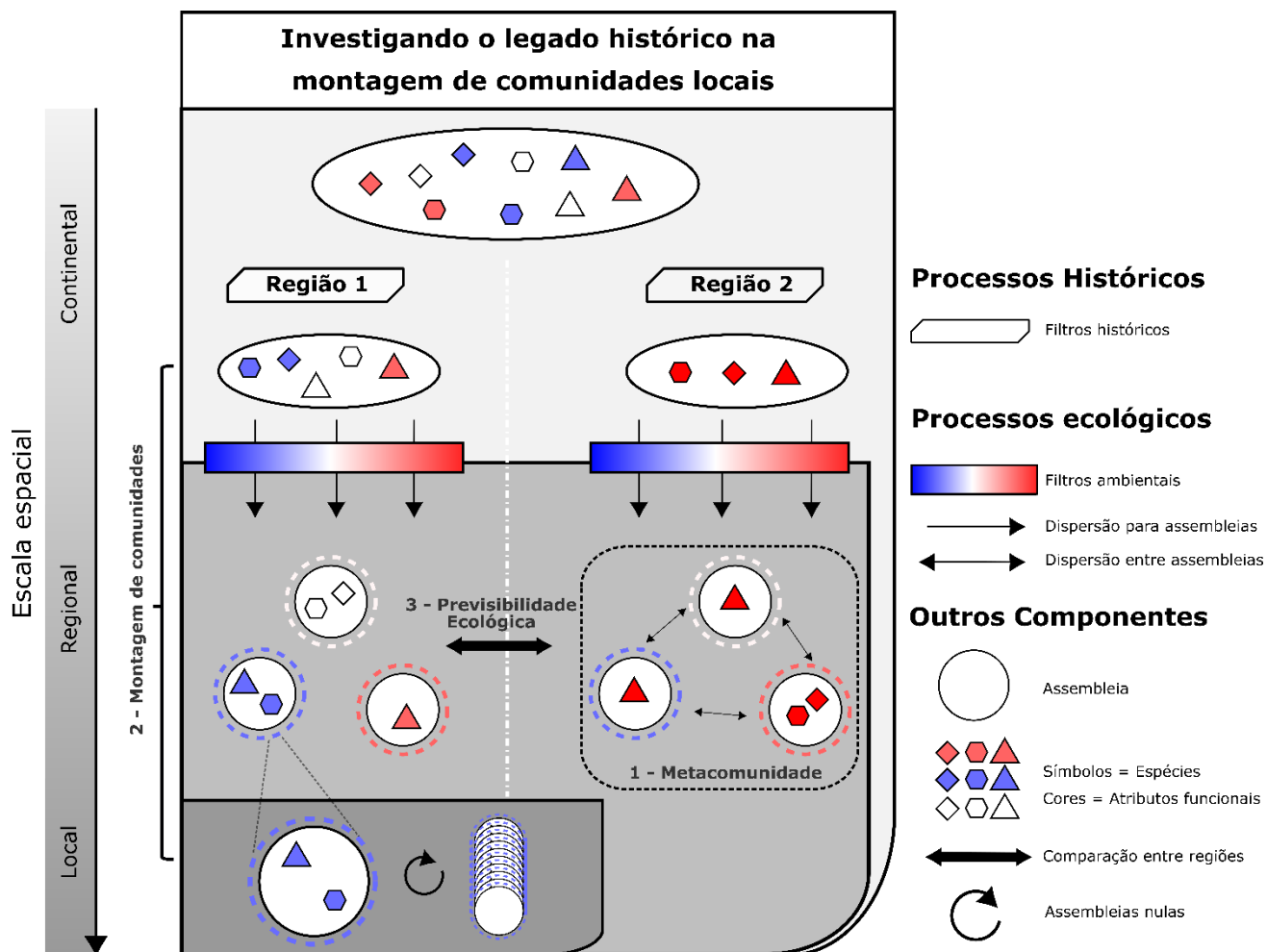
## Introdução geral

### *A importância do legado histórico na montagem de comunidades locais*

Identificar os mecanismos pelos quais comunidades biológicas são estruturadas permanece como um dos objetivos centrais da Ecologia de Comunidades (Vellend 2016; Rapacciolo and Blois 2019). Essa representa uma das tarefas mais complexas dentre os objetos de estudo dos ecólogos, visto que diferentes mecanismos atuando em diferentes escalas espaciais e temporais são capazes de modular a composição e diversidade de comunidades locais (Chase 2003; Warren et al. 2014). Em largas escalas, processos históricos e biogeográficos, expressos fundamentalmente através de eventos de especiação, extinção e dispersão (Vellend, 2016), moldam a diversidade e composição do conjunto regional de espécies (i.e., *pool* regional). Partindo para escalas menores, processos ecológicos, baseados em seleção ou filtros abióticos e bióticos (Vellend, 2016), determinam quais espécies oriundas do *pool*, e que chegaram à determinada localidade, são capazes de coexistir localmente (HilleRisLambers et al. 2012). A partir dessa visão hierárquica, é possível inferir que a estruturação local de comunidades deve ser moldada pela interação entre processos históricos e ecológicos (Figura 1). Assim, uma questão chave não seria somente apontar o principal mecanismo pelo qual as comunidades são estruturadas, mas também como tais mecanismos interagem para moldar os padrões locais de biodiversidade, assim como compreender até que ponto tais padrões são replicáveis entre diferentes regiões biogeográficas. A interação entre processos históricos e ecológicos pode se dar de diversas formas e afetar diferentes aspectos da estrutura de comunidades, tais como a organização de metacomunidades (**Capítulo 1**), regras de montagem (**Capítulo 2**) e até mesmo a previsibilidade ecológica frente às condições ambientais (**Capítulo 3**).

Por muito tempo, estudos em Ecologia de comunidades foram restritos à abordagem puramente taxonômica, que, embora de extrema importância, contemplam apenas uma das facetas da biodiversidade. No entanto, as espécies apresentam diferentes requerimentos ecológicos que modulam suas respostas frente a diferentes processos ecológicos (McGill et al. 2006; Mouillot et al. 2013). Tais requerimentos estão diretamente associados ao conjunto de atributos funcionais (do inglês *functional traits*) característico de cada espécie. Estes são definidos por quaisquer características mensuráveis (e.g., morfológicas, fisiológicas, comportamentais) que influenciam direta ou indiretamente as respostas dos organismos às variações ambientais ou outros organismos, e podem ter efeito sobre o funcionamento dos ecossistemas (Violle et al. 2007; Teresa et al., 2021). A importância de se incluir a abordagem funcional em estudos ecológicos se dá pelo suposto maior poder preditivo em comparação à abordagem taxonômica (mas ver Saito et al. 2020). Essa ideia é sustentada pelo fato de que incorporar as diferenças ecológicas entre as espécies pode tornar mais claro o entendimento dos padrões observados de distribuição e coexistência de espécies que dificilmente seriam evidenciados apenas ao se considerar apenas a abordagem taxonômica (Díaz and Cabido 2001). Por não considerar a identidade das espécies em si, mas sim suas características ecológicas, a abordagem funcional também possibilita a comparação entre comunidades historicamente diferentes e com baixa similaridade de composição de espécies. Por exemplo, responder se processos históricos promovem diferenças na composição de espécies de plantas entre comunidades de regiões Temperadas e Tropicais pode parecer óbvio (i.e., possivelmente nenhuma espécie, ou bem poucas, compartilhada entre as regiões), enquanto a mesma pergunta sob uma óptica funcional pode culminar em

inúmeras hipóteses ecológicas plausíveis. Reconhecemos que tal exemplo não se encaixa perfeitamente nas principais predições de estudos funcionais, já que por essência assumem que tanto a estrutura como a diversidade funcional são fortemente explicadas por processos locais, em parte negligenciando o papel de processos históricos/biogeográficos (Poff 1997; Díaz and Cabido 2001). No entanto, nessa tese encontramos algumas evidências que podem ‘balançar’ a presumida previsibilidade da abordagem funcional frente a fatores locais (e.g., tipos de habitat), bem como expandir a ideia de que processos históricos podem influenciar os padrões de estrutura/diversidade funcional dentro de comunidades locais, assim como dificultar a sua replicabilidade entre regiões.



**Figura 1.** Quadro esquemático utilizado ao longo da tese para investigar a importância do legado histórico na estrutura de comunidades locais dentro (1 – Metacomunidade; 2 – Montagem de comunidades) e entre duas regiões biogeográficas (3 – Previsibilidade ecológica). A montagem de comunidades (2) é investigada para cada comunidade local com a utilização de modelos nulos – procedimento estatístico que cria comunidades nulas onde processos ecológicos de interesse (e.g., limitação de dispersão, seleção de nicho, interações bióticas) podem ser controlados.

A teoria de metacomunidades prediz que a estrutura de comunidades locais é explicada pelo balanço entre processos baseados em nicho e em dispersão (Leibold et al. 2004). Nesse contexto, distância espacial e condições ambientais locais determinam quais espécies podem colonizar e

eventualmente se estabelecer localmente. Nas últimas décadas, uma grande quantidade de estudos vem aplicando a teoria de metacomunidades nos mais diversos ecossistemas e grupos taxonômicos (Lansac-Tôha et al. 2021). No entanto, uma das principais meta análises sobre o tema (Cottenie 2005) em conjunto com estudos empíricos (Gianuca et al. 2017) têm diminuído nosso entusiasmo ao longo dos anos por demonstrar que uma única conclusão geral ainda não pode ser desenhada a partir dos fatores ambientais e espaciais. Adicionalmente, a dinâmica de metacomunidades pode ser ainda mais complexa se assumirmos que os padrões atuais de coocorrência de espécies também são explicados por processos históricos e biogeográficos (Leibold et al. 2010). Tais eventos afetaram a configuração do passado, definindo o arranjo espacial do *pool* de espécies de uma região (Cavender-Bares et al. 2009). Interessantemente, essa influência do passado pode criar padrões de distribuição de espécies comumente associados com processos baseados em nicho. Ou seja, a partir de um ponto de vista ecológico, a coexistência de espécies em uma região pode ser interpretada com processos baseados em nicho, enquanto a partir de um ponto de vista histórico-filogenético o mesmo padrão pode ser interpretado como um efeito alopatrico (Wiens and Donoghue 2004). Assim, o conhecimento histórico-filogenético pode promover informações relevantes sobre como a dinâmica de metacomunidades é organizada, além de processos baseado em nicho e dispersão. Este foi o fio condutor do **Capítulo 1** desta tese, que utilizou peixes de riachos da Caatinga como modelo de estudo e é intitulado **“How are local fish communities structured in Brazilian semiarid headwater streams?”**.

Por trás da dinâmica de metacomunidades existe um ramo de pesquisas ecológicas que investiga como comunidades locais são estruturadas a partir do *pool* regional de espécies, ou seja, como ocorre a montagem de comunidades locais (Weiher and Keddy 1995). Os principais mecanismos investigados na montagem de assembleias são aqueles responsáveis por explicar os padrões locais de coocorrência das espécies, sendo estes supostamente melhor revelados ao utilizarmos uma abordagem baseada em atributos funcionais (Weiher et al. 2011). Para isso, se utiliza um quadro hierárquico onde processos históricos moldam a composição do *pool* regional de espécies, que é posteriormente filtrado por condições ambientais para definir o *pool* local de espécies (Pärtel et al. 2011). A partir desse *pool* local, interações bióticas determinam quais espécies são capazes de coexistir (de Bello et al. 2012). A soma desses filtros molda a composição de espécies nas comunidades locais e, portanto, a distribuição de atributos funcionais que variam ao longo de um gradiente de baixa (subdispersão de atributos; do inglês *trait underdispersion*) ou alta variação (sobredispersão de atributos; *trait overdispersion*). Embora a montagem de comunidades inicie com a formação do *pool* de espécies a partir de processos históricos, os padrões de *overdispersion* e *underdispersion* são frequentemente relacionados com fatores ecológicos, tais como tipos de habitat local (Perronne et al. 2017) e interações competitivas entre espécies com requerimentos ecológicos semelhantes (Mudrák et al., 2015). Contudo, qualquer modificação no *pool* de espécies pode produzir diferentes padrões de distribuição dos atributos funcionais, mesmo em locais com condições ambientais similares (Götzenberger et al. 2012). Assumindo que a composição e diversidade do *pool* regional de espécies é originada principalmente por processos históricos (Carstensen et al. 2013), é possível inferir que a montagem de comunidades pode variar consideravelmente entre regiões com diferentes histórias evolucionárias. Essa hipótese foi investigada no **Capítulo 2**, que teve as assembleias de peixes de riachos

da Amazônia como modelo de estudo e foi intitulado “**Historical and ecological drivers of community assembly of the Amazonia stream fish assemblages**”.

Estimar a importância relativa de processos históricos e ecológicos em moldar a dinâmica de metacomunidades e de montagem de comunidades locais dentro de regiões biogeográficas é de extrema importância para entendermos como eventos passados se conectam com o presente para moldar os padrões contemporâneos de biodiversidade. No entanto, para alcançarmos a tão sonhada capacidade de generalização dentro da Ecologia (*sensu* Lawton 1999) é preciso investigar se comunidades de diferentes regiões respondem de forma semelhante frente a mudanças do ambiente. Nesse contexto, condições do habitat local supostamente promovem padrões consistentes entre regiões biogeográficas, por selecionar deterministicamente espécies com determinadas características funcionais (McGill et al. 2006). Dessa forma, seria plausível esperar que comunidades com condições de habitat local similar tenderiam a apresentar estrutura funcional similar, independentemente de seus passados históricos (Poff 1997). Mas e se tais comunidades possuísem diferentes ‘arsenais’ de combinações de atributos funcionais disponíveis regionalmente para ocorrência local? Isso seria possível se essas comunidades estivessem inseridas em regiões com fortes diferenças na estrutura funcional do *pool* regional de espécies (Spasojevic et al. 2018). Assumindo que atributos funcionais refletem a habilidade dos indivíduos para crescer e se reproduzir em determinado ambiente (Violle et al. 2007), diferenças na estrutura funcional (e.g., diversidade e composição de atributos funcionais) do *pool* de espécies entre regiões, de fato, podem ‘bagunçar’ a esperada e previsível relação entre condições de habitat e estrutura funcional das assembleias locais. Por exemplo, eventos históricos que promovem altas taxas de extinção ao longo do tempo (e.g., mudanças climáticas) podem eliminar, de forma não determinística, espécies com combinações de atributos fortemente relacionados com a exploração de habitats complexos (e.g., raízes em ambientes aquáticos) em uma região, mas não em outra. Assim, baixo poder preditivo seria observado ao investigar se locais com alta complexidade ambiental produzem assembleias funcionalmente similares entre essas duas regiões. Embora formulada sob um âmbito puramente teórico, essa hipótese pode ser testada ao se comparar locais com condições de habitat similar em diferentes regiões biogeográficas, porém com diferentes histórias evolutivas. Caso as diferenças na estrutura funcional do *pool* de espécies entre regiões de fato influenciem a montagem de comunidades locais, espera-se que haja maior poder preditivo acerca do papel de determinadas condições do habitat em moldar a estrutura funcional das assembleias ao se comparar conjuntos de locais com estrutura funcional do *pool* de espécies similar. Essa hipótese geral foi testada no **Capítulo 3** da tese, que utilizou como modelo de estudo a ictiofauna de riachos da Amazônia e da Caatinga, e foi intitulado “**The functional structure of species pools explains idiosyncratic assembly patterns among biogeographical regions**”.

Para investigar as três questões citadas acima é necessário um grande conjunto de dados distribuídos entre regiões com diferentes histórias evolucionárias, ao mesmo tempo que possui informações refinadas de condições locais abióticas (e.g., tipos de habitat) e bióticas (e.g., abundância, composição e atributos funcionais das espécies). Para isso, utilizamos um conjunto de dados de 400 riachos nos biomas brasileiros: Amazônia (n=340) e Caatinga (n=60). Esses biomas possuem diferentes raízes evolucionárias e uma boa descrição de seus passados históricos, ao mesmo tempo em que possuem riachos com uma alta variação de características de habitat (ver abaixo).



### *História evolucionária dos biomas Caatinga e Amazônia*

A história evolucionária das bacias hidrográficas da América do Sul é repleta de eventos geológicos que isolaram, conectaram ou mudaram os cursos dos corpos d'água, o que influenciou drasticamente a riqueza e composição regional da fauna de água doce (Hubert and Renno 2006). Nas bacias hidrográficas do Norte-Nordeste do Brasil, tais eventos são relativamente bem descritos (Pôrto et al. 2004; Hoorn et al. 2010). Por exemplo, o que hoje conhecemos como o bioma da Caatinga, característico por seu clima semiárido, já foi um ambiente de transição entre as florestas Amazônica e Atlântica (Carnaval and Moritz 2008). No entanto, após o último período glacial (~12 mil anos atrás), o clima da região mudou de tropical úmido para semiárido, forçando o recuo das florestas densas supracitadas (Pôrto *et al.*, 2004). Como consequência dessa mudança, atualmente observa-se baixa diversidade regional e local de peixes de riachos na Caatinga (Rodrigues-Filho et al. 2018). Por outro lado, o bioma Amazônico apresentou relativa estabilidade climática após o último período glacial, sendo um dos fatores que explicam sua maior diversidade regional e local da ictiofauna de riachos (Hoorn et al., 2010).

No entanto, a história evolutiva da hidrografia da Amazônia foi drasticamente remodelada desde o Paleogeno (~ 65 milhões de anos atrás) (Hoorn et al. 2010). Por exemplo, paralelamente à intensificação do soerguimento do Andes, um vasto sistema de lagos (i.e., sistema “Pebas”) se formou na região mais a Oeste da Amazônia, se estendendo até a região central, onde foi barrado pelo paleoarco do Purus (~ 25 milhões de anos atrás). Estima-se que o sistema Pebas também tenha favorecido a grande diversificação da fauna de água doce amazônica. Assim, essa região representa um dos berços da biodiversidade de água doce da Amazônia. Há aproximadamente 5 Mya, esse grande sistema de lagos se converteu em um regime fluvial, correndo para as regiões mais a Leste da Amazônia, que por consequência foi em parte colonizada pelas espécies provenientes do Oeste. Assim, as bacias do Leste são compostas por menor quantidade de espécies em comparação às do Oeste. Em adição, as bacias do Leste foram banhadas por água do mar (~5 Mya) o que possivelmente promoveu a extinção de porção significativa da fauna de água doce (Haq et al. 1987). A partir desse cenário, é possível assumir que ao longo do gradiente Oeste-Leste da Amazônia existe uma diminuição na riqueza regional de peixes de água doce, explicado pela diminuição das taxas de especiação e aumento das taxas de extinção (Oberdorff *et al.*, 2019).

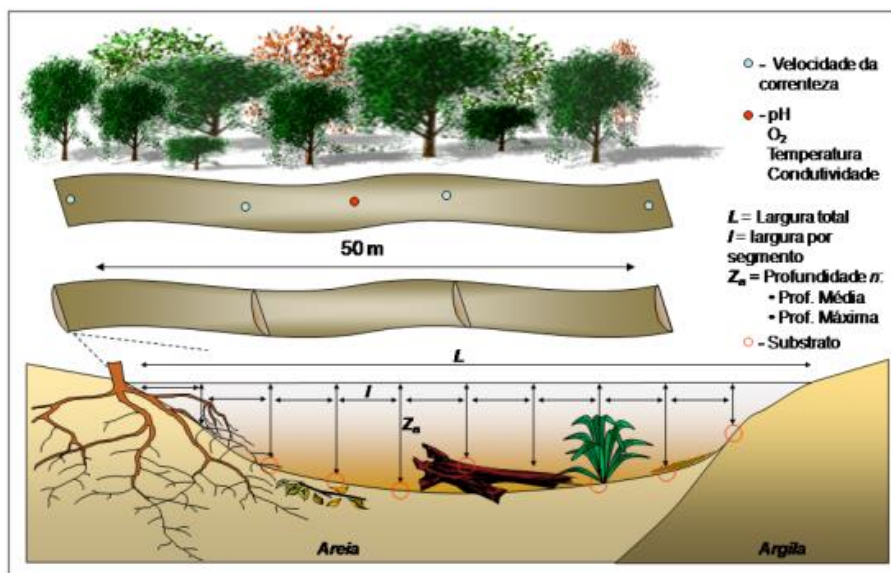
Tais eventos evolutivos dentro e entre os biomas da Amazônia e da Caatinga influenciaram fortemente os padrões de diversidade regional para a ictiofauna de água doce (Rodrigues-Filho et al. 2018; Oberdorff et al. 2019). No entanto, pouco se sabe sobre como tais eventos podem influenciar a estrutura local das assembleias biológicas. Para isso, estudos comparativos ou cobrindo regiões com diferentes histórias evolucionárias podem ser considerados uma peça-chave para melhor entendermos como o passado se conecta com o presente. Nesse sentido, ecossistemas de riachos representam um excelente modelo de estudo.

### *Riachos da Amazônia e da Caatinga*

Riachos são considerados qualquer corpo de água corrente, de pequeno porte, e que pode ser atravessado a pé (Caramaschi et al. 2021). Por muito tempo tais ecossistemas foram negligenciados em

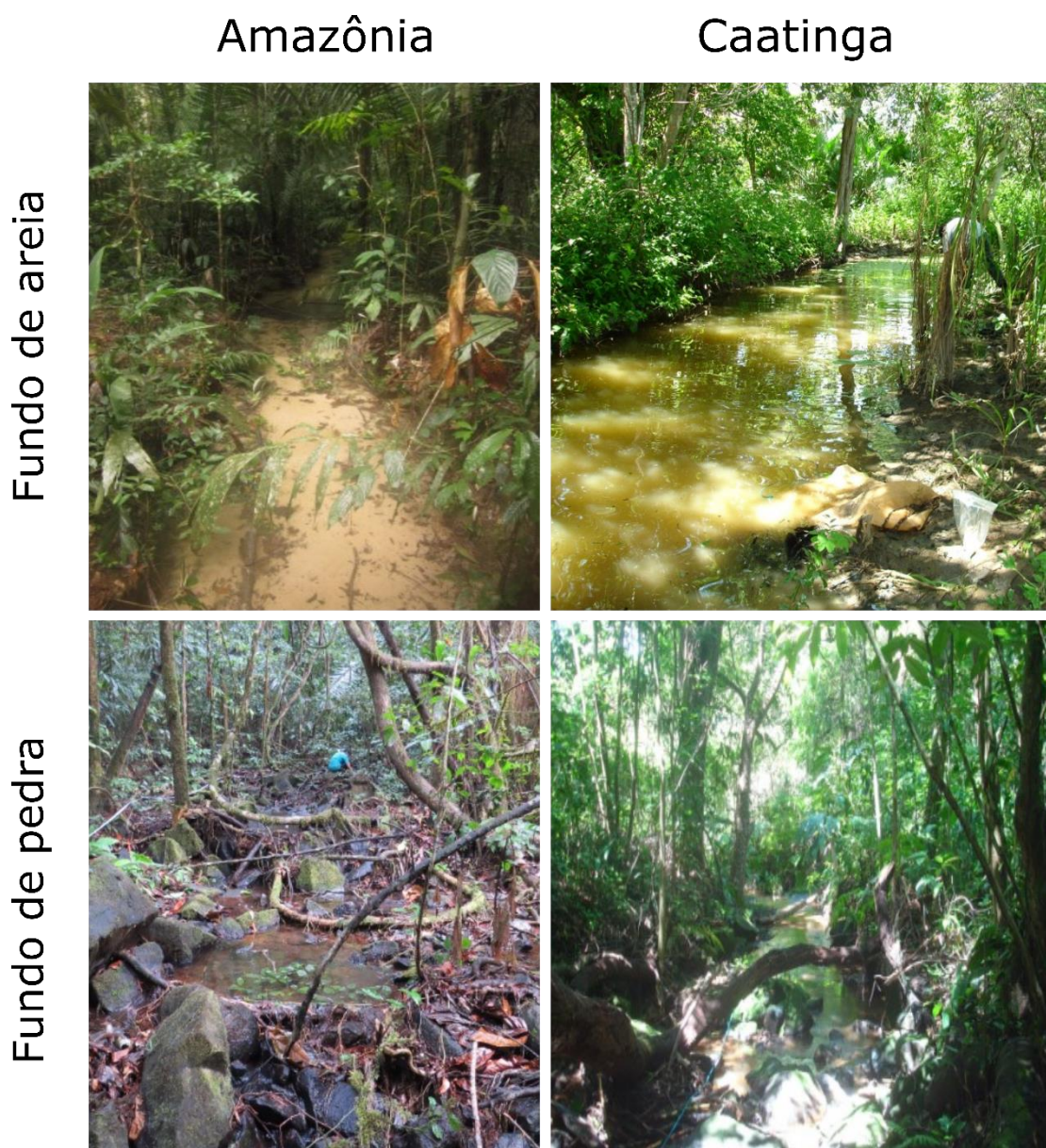
comparação a ecossistemas terrestres, devido a equivocada percepção que ambientes tão pequenos, e em muitos casos intermitentes, não seriam capazes de comportar alta diversidade biológica (Datry et al. 2014). Atualmente tal alegação deve soar estranho sob os ouvidos de pesquisadores que, após muitas décadas de árduo esforço, vêm mostrando a partir de estudos de história natural e padrões de distribuição que ecossistemas de riachos são de extrema importância para a manutenção de uma altíssima biodiversidade e para a conservação em escala local e regional (Carvalho and Tejerina-Garro 2015, Leal et al. 2020).

Especificamente no Brasil, o interesse em ecossistemas de riachos tem aumentado de forma exponencial a partir dos anos 2000, onde as regiões Norte e Sudeste concentram a maior densidade de estudos realizados (Dias et al. 2016). Não por acaso, nessas regiões existem grupos de pesquisadores que durante anos têm realizado amostragem de aspectos físicos (e.g., estrutura do canal e tipos de substrato) e bióticos (e.g., composição e abundância de espécies) de forma padronizada, o que favoreceu a construção de robustos bancos de dados e vem possibilitando a realização de estudos em uma maior escala espaço-temporal. O sucesso do protocolo padronizado de amostragem em riachos nas regiões Norte e Sudeste, em conjunto com o espírito colaborativo, incentivou pesquisadores de outras partes do Brasil a iniciarem a construção de seus bancos de dados, como por exemplo na região Nordeste (bioma Caatinga). Padronizações são realizadas entre regiões (Figura 2), tornando possível a elaboração de estudos que conectam diferenças históricas (e.g., características do bioma) e ecológicas (e.g., estrutura física do riacho). Em outras palavras, os riachos brasileiros podem prover uma ótima oportunidade para a realização de estudos que conectam processos históricos e ecológicos bem como suas interações para o entendimento da montagem de comunidades locais.



**Figura 2.** Representação esquemática dos métodos de coleta de variáveis ambientais locais utilizadas em riachos da Amazônia e da Caatinga. A unidade amostral é definida por um trecho de 50 m de extensão (sítio). Foram considerados fatores ambientais locais característicos estruturais do sítio (largura, profundidade, vazão, velocidade da correnteza e tipo de substrato) e físico-química da água (temperatura,  $[O_2]$ , pH, e condutividade). A mensuração de tais fatores seguiu a metodologia utilizada em Mendonça et al. 2005.

Tanto na Amazônia como na Caatinga, os riachos utilizados nessa tese são oligotróficos e em sua maioria correm dentro de vegetação densa. Com relação as dimensões do canal, é comum observar riachos estreitos e rasos (< 5 m de largura e < 1 m de profundidade) (Mendonça et al. 2005). O substrato é predominantemente composto por areia e liteira fina, com grande volume de troncos e raízes (fundo de areia na Figura 3). Por outro lado, nos dois biomas existem regiões elevadas com riachos apresentando com alta velocidade de correnteza e fundo composto por cascalhos, pedras e rochas. Na Amazônia, tais riachos são comumente encontradas na Amazônia central, bacia do rio Uatumã, enquanto na Caatinga são encontrados em regiões de chapadas, conhecidas popularmente como *brejos de altitude* (Pôrto et al. 2004) (fundo de pedra na Figura 3).



**Figure 3.** Riachos de cabeceiras na Amazônia (esquerda) e na Caatinga (direita). Fonte das imagens: R. P. Leitão, C. A. S. Rodrigues-Filho, L. Stegmann.

*Atributos funcionais em peixes de riachos*

A água possui maior densidade do que o ar, assim, a locomoção em ambientes aquáticos exige maior gasto energético do que em ambientes terrestres. A realização de comportamentos básicos (e.g., locomoção, aquisição de recursos alimentares e exploração de habitats) para organismos aquáticos devem seguir as leis da hidrodinâmica (Gatz 1979). Apesar de lógico, esse fato carrega importantes expectativas sobre a ecologia funcional nesses ambientes. Por exemplo, a ecologia funcional é baseada na premissa de que indivíduos com características que aumentam sua aptidão (do inglês *fitness*) em explorar o ambiente (e.g., exploração de habitat ou aquisição de recursos) devem apresentar maior abundância do que indivíduos com características que diminuem sua aptidão (Violle et al. 2007). Utilizando essa definição para peixes de riachos é possível inferir que características que reduzem o gasto energético para comportamentos básicos podem ser consideradas atributos funcionais. Portanto, tais atributos seriam caracterizados como de resposta ao ambiente, podendo ser mensurados por análises ecomorfológicas (Villéger et al. 2017).



**Figure 4.** Alguns exemplares de peixes capturados em riachos da Amazônia e da Caatinga. Fonte das imagens: Jorge Iván Sánchez-Botero, Lis Stegmann. <sup>1</sup>*Callychthys callychthys*; <sup>2</sup>*Hoplias malabaricus*; <sup>3</sup>*Corydoras garbei*; <sup>4</sup>*Helogenes marmoratus*; <sup>5</sup>*Apistogramma steindachneri*; <sup>6</sup>*Parotocinclus haroldoi*;

<sup>7</sup>*Ituglanis amazonicus*; <sup>8</sup>*Steinacachnerina notonota*; <sup>9</sup>*Trachelyopterus galeatus*; <sup>10</sup>*Pyrrhulina brevis*;  
<sup>11</sup>*Hemigrammus marginatus* <sup>12</sup>*Hypostomus jaguribensis*.

Estudos utilizando análises ecomorfológicas como um indicativo para atributos funcionais são comuns para a ictiofauna de riachos (Ribeiro et al. 2016; Leitão et al. 2018; Brejão et al. 2018; Benone et al. 2020). Além disso, são de grande valia para estudos realizados em regiões mega diversas, tais como na Amazônia, onde a informação sobre história natural das espécies é extremamente escassa (Dagosta and Pinna 2019), ou em estudos que comparam regiões com baixa similaridade de composição regional de espécies, tais como Amazônia e Caatinga (Rodrigues-Filho et al. 2018). Por exemplo, a riqueza estimada de peixes de riacho na Amazônia é de aproximadamente 1200 espécies, enquanto na Caatinga é de aproximadamente 150 (Dias *et al.*, 2021) (Figura 4). Assim, a partir de análises ecomorfológicas é possível investigar se riachos com condições ambientais similares, mas localizados em regiões distintas, são compostos por espécies com padrão morfológico similar (Bower and Winemiller 2019), permitindo a realização de estudos em larga escala espacial. Tais estudos são extremamente escassos, como observado por Teresa et al. (2021) que a partir de levantamento de literatura para a ictiofauna de riachos brasileiros, registraram apenas um artigo científico comparando explicita e diretamente a estrutura funcional de peixes de riachos entre regiões biogeográficas.

## **OBJETIVO GERAL**

O objetivo geral dessa tese é investigar como processos históricos e ecológicos interagem para moldar a estrutura e diversidade funcional de assembleias de peixes de riachos em dois biomas brasileiros:

Amazônia e Caatinga. Especificamente, pretendo:

- Investigar a importância relativa de fatores ambientais, espaciais e de história filogenética em explicar a dinâmica de metacomunidades em peixes de riachos do semiárido brasileiro;
  
- Investigar como fatores históricos e ecológicos interagem para determinar a diversidade funcional de peixes de riachos da Amazônia;
  
- Determinar se a diferença na estrutura funcional do pool de espécies modula a relação entre condições ambientais locais e estrutura funcional de assembleias de peixes de riachos da Amazônia e da Caatinga.

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**CAPÍTULO 1**

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Carlos Alberto de Sousa Rodrigues-Filho, Ronaldo César Gurgel-Lourenço, Luís Artur Valões Bezerra, Edson Fontes de Oliveira, Rafael Pereira Leitão, Danielle Sequeira Garcez, Jorge Iván Sánchez-Botero. How are local fish communities structured in Brazilian semiarid headwater streams? Manuscrito publicado na revista *Hydrobiologia*.

## **How are local fish communities structured in Brazilian semiarid headwater streams?**

Short title: Fish assemblages in Brazilian semiarid headwaters

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**Abstract** Environmental and spatial factors are known as the main determinants of community variation in aquatic organism. However, historical factors may interact with local processes to regulate community structure patterns. Here we compared historical, environmental, and spatial factors in a multi-scale approach in order to identify the main drivers structuring species composition and functional diversity of fish communities in forest enclaves across three hydrographic basins in semiarid Brazil. We initially modeled spatial structure within each basin using asymmetric eigenvector maps (AEM). We then partitioned the explanation of the variation in local community structure into three groups of predictor variables: (1) environmental variables, (2) spatial variables, and (3) phylogenetic history. Biogeographical bias was assessed using a basin identity matrix as covariable. The combination of 1, 2 and 3 explained the variation in species composition, while pure spatial, phylogenetic, and environmental components explained the distribution of functional groups and their nested patterns. Our findings confirmed the importance of phylogenetic history, as well as the usefulness of robust methods in community studies in refining explanations of the processes determining variation in species composition and functional groups.

**Keywords** Caatinga biome; freshwater fish; historical constraints; functional groups; spatial analysis; environmental filters.

## Introduction

The assembly of communities is a central issue within ecology, with classical approaches assuming niche-based processes and dispersion as the main drivers structuring communities across most spatial scales (Hubbell, 2001; Leibold et al., 2004). In addition, historical processes affect the configuration of the past, defining the spatial arrangement of ecosystems (Hubert & Renno, 2006), and consequently the regional pool of species capable of colonizing local communities (Cavender-Bares et al., 2009). As a result, the phylogenetic structure of communities, the patterns of species coexistence (Cavender-Bares et al., 2009), and the diversity of functional traits within species pool are closely related to the history of a given region (Olden et al., 2010; Rodrigues-Filho et al., 2018). This view is based on the assumption that biogeography and phylogenetic history are, together, the main structuring forces acting on communities at the regional scale (Peres-Neto et al., 2012; Sternberg et al., 2014). For example, patterns purely linked to species dispersion limitation (mass effect or neutral dynamics) could be due to historical legacies (i.e. tectonic movements; Peres-Neto & Legendre, 2010). Similarly, patterns of species coexistence commonly interpreted as a consequence of environmental filters (sorting) may, in fact, result from allopatric effects (Wiens & Graham, 2005). In this context, the knowledge of phylogenetic history can provide additional information on how niche-based processes and dispersion structure current local communities (Sternberg et al., 2014; Castillo-Escrivà et al., 2017).

Aquatic systems are ideal for testing the effects of historical, niche-based and dispersion processes, since they show discrete spatial distribution and have extensive environmental gradients (Heino, 2013). In such systems, in addition to the action of historical filters, processes based on niche breadth and dispersion capacity can act together to structure local communities across a variety of spatial scales (Tonn, 1990). From the niche perspective, environmental conditions would select species with similar phenotypic characteristics (Poff, 1997). On the other hand, the dendritic configuration of river systems can act as a barrier to the movement of species with low dispersion capacity (Heino et al., 2015). Thus, taken together, niche-based process and dispersal limitation supposedly are the main factors determining the spatial structure of stream fish communities (Vitorino Júnior et al., 2016).

In headwaters, great hydrological variation coupled with high environmental heterogeneity favors processes based on niche (Landeiro et al., 2011; Zbinden & Matthews, 2017), although contrary results have been reported (Cetra et al., 2017). In part, these contradictory results may be explained by the complex dynamic of colonization and extinction typically found in headwaters, where flash flood events are common (Taylor and Warren, 2001). This dynamic can generate a pattern of nested subgroups in headwater streams. However, to better understand the complexity of this relationship, it is necessary to investigate the other facets of biodiversity (McGill et al., 2006). Functional ecology is an aspect of biodiversity which adds complementary information to taxonomic approaches, especially by providing a mechanistic link to buttress explanations based solely on environmental conditions (Heino et al., 2007; Sternberg et al., 2014; Zorzal-Almeida et al., 2017; Tolonen et al., 2018). In addition, grouping species based on functional traits (related to performance or fitness) has proven useful in the development of generalized ecological models (Teresa & Casatti, 2012; Arantes et al., 2017; Henriques et al., 2017). This is explained by the relation between the functional characteristics of the species and its environmental requirements and dispersion capacity (Campos et al., 2018). Fish are a good model group with which to

examine such relationships since they have a wide range of trophic associations, habitat uses and body sizes (Villéger et al., 2017).

The South American ichthyofauna is hyper-diverse and one of the best models for the assessment of functional relationships (Toussaint et al., 2016). Marine transgressions, tectonics, climate change and historical connections between river basins have been the principle events shaping fish diversity and distribution in the Neotropics (Hubert & Renno, 2006; Ribeiro, 2006; Dias et al., 2014). Humid forest enclaves in semiarid Brazil (Caatinga biome) are a very particular system due to the long-term disturbances occurring during their formation (Pôrto et al., 2004). However, apart from their high levels of endemism, little is known about the ecology of stream fishes in such enclaves (Rodrigues-Filho et al., 2016; but see Gurgel-Lourenço et al., 2017).

In this study we assessed: (i) the relative importance of environmental, spatial, and historical events in taxonomically and functionally structuring stream-fish communities, (ii) the relation between environmental gradients and the distribution of species and functional groups, and (iii) whether environmental variation is responsible for the nested patterns of species distribution and functional groups. We expected variations between the communities in humid forest enclaves within Caatinga to be explained by a suite of opposing forces. In the taxonomic approach, historical events should be of primary importance, whereas environmental conditions will be better at explaining functional group distribution. Moreover, considering the importance of basin identity to river fishes (Heino et al., 2017), and their association with factors influencing regional biogeographical aspects (Benone et al., 2017), we expected the results of the taxonomic approach to be basin-specific. We also tested whether environmental conditions generate taxonomic and functional nesting patterns and expected spatial determinants to explain the local distribution of species and functional groups within the species pool.

## **Methods**

### *Study location and sampling*

We sampled 26 streams of the Caatinga highlands of Araripe and Ibiapaba, two plateaus climatically and hydrologically defined as tropical forest enclaves. Such rainforests are typically found in tablelands up to 1,000 m elevation, with annual rainfalls (~1,000 mm) well above the average for semiarid regions. Over the last 25,000 years, these forests have become uncommon due to the synergy between drought and anthropic activity, exacerbated by the short duration of the rainy season (usually from January to May) in northeastern Brazil (Brasil et al., 2016; Rito et al., 2017). The investigated streams were perennial, despite a considerable decrease in flow during the dry season (Rosa & Groth, 2004). During the rainy seasons in 2011-2013, we sampled streams from three river basins: Jaguaribe (J), São Francisco (F) and Coreau (C), the first two on the Araripe Plateau, the third on the Ibiapaba Plateau (Figure 1; Table S1.1 of Appendix 1).

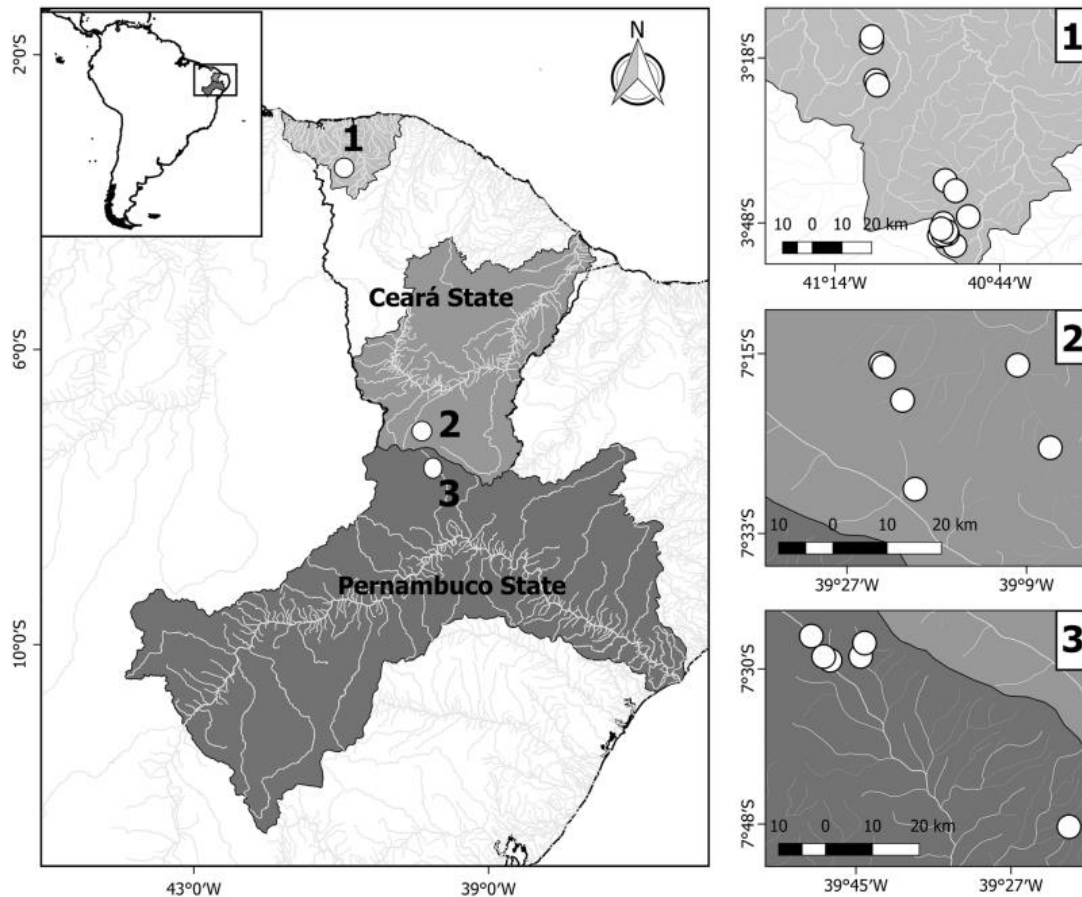


Figure 1 Sampling points (white circles) and riverine basins (1 - Coreaú; 2 - Jaguaribe; 3 - São Francisco) in forest enclaves in semiarid Brazil.

Sampling occurred on 50-m stretches of the stream, following a standardized protocol designed by Mendonça et al. (2005). We blocked the extremities of each stretch with 12 mm nets to prevent fish from escaping, then defined four equidistant transects in which the following environmental conditions were assessed: average width (m), depth (m). Water velocity ( $\text{m}\cdot\text{s}^{-1}$ ) in the channel was measured three times in each transect, using the distance traveled by a Styrofoam ball. We recorded water temperature ( $^{\circ}\text{C}$ ) and dissolved oxygen ( $\text{mg}\cdot\text{L}^{-1}$ ) once, sampling downstream from the stretches. A GPS was used to determine geographic coordinates and elevation (m). Vegetation coverage (%) was calculated based on 16 b/w photographs of the canopy, using a digital camera fitted with 5.8-23 mm lenses (Mendonça et al., 2005). Area ( $\text{m}^2$ ) and average depth (m) of each stretch were used to determine habitat volume ( $\text{m}^3$ ). Relative substrate composition (%) was determined using the classification of Gonçalves & Braga (2012): pebble/gravel (1-10 mm; Pb), coarse sand (0.1-1 mm; Cs), fine sand (0.05-1 mm; Fs) and silt/clay ( $< 0.05$  mm; Sc) (see Table S1.2 of Appendix 1 for a summary of environmental data).

#### *Taxonomic and functional data*

Fish were captured with cast nets ( $5.3\text{ m}^2$ ; 14 mm mesh), sieves ( $0.7\text{ m}^2$ ; 1 mm mesh) and seine nets ( $1.3\text{ m}^2$ ; 2 mm mesh) in a fishing effort of four person-hours. Specimens were euthanized by immersion in an anesthetic solution of eugenol and preserved in a 10% formalin solution, followed by storage in



70% alcohol. Specimens were identified to species level (Table S1.3), and voucher specimens deposited in the fish collection of the Universidade Federal do Rio Grande do Norte (UFRN).

Classification of species into functional groups used six traits (diet, feeding tactic, vertical compartment, body mass, current flow, and substrate specificity) and 26 trait categories (Sabino & Zuanon, 1998; Teresa & Casatti, 2012; Brejão et al., 2013; Table 1 and Table S3.1 of Appendix 3). For trait categories, we adopted a binary approach when characterizing each species. When information at the species level was not available in the literature (30% of the species), we used a genus-level classification. These traits were selected due to their mechanistic relation with species locomotion capacity (Blanchet et al., 2010), resource use and microhabitat exploration (Teresa & Casatti, 2012; Rodrigues-Filho et al., 2017), these being key aspects in dispersal and niche-based processes.

Table 1 Traits and 26 functional categories used to group fishes sampled in enclaves of tropical forest in semi-arid Brazil, with the abbreviations used in subsequent analyses.

Traits	Category	Abbreviation
Diet	detrivore	det
	aquatic insectivore	a.ins
	herbivorous insectivore	h.ins
	invertivore	inv
	omnivore	omn
	piscivore	pis
Feeding tactic	water column	wcol
	substrate speculation	sspe
	ambusher	amb
	grazer	gra
	stalker	sta
	night active	nig
	surface	sur
Vertical compartment	nektonic	nek
	nektobenthic	nekt
	benthic	ben
Current flow	slow	slo
	intermediate	int.flo
	fast	fas
Body mass	very light (<0.001g)	v.lig
	light (0.001-1g)	lig
	intermediate (1-2.5g)	int.bod
	heavy (>2.5g)	hea
Specify for substrate	low	low
	intermediate	int.sub
	high	hig

As recommended by Pillar & Sosinski (2003) and Dumay et al. (2004), functional group classification included three steps, in order to minimize subjectivity bias. We first calculated Pearson correlation coefficients among trait categories to determine if the selected traits reflected informative and complementary functions within the fish assemblage (Appendix 2). Subsequently, and to reduce the dimensionality of functional space, we performed a principal coordinates analysis (PCoA) based on a Gower's distance matrix of species traits (Pavoine et al., 2009). We selected the first nine eigenvectors (broken-stick explanation percentage: 71.7%; Table S3.2 of Appendix 3) and submitted it to non-

hierarchical cluster analysis (*k*-means clustering). Then, based on functional space, five functional groups were defined by minimizing the sum of squared Euclidian distances between the species and the centroid of the groups (Table 2; Table S3.3 and Figure S3 of Appendix 3).

Table 2 Taxonomic composition within each functional group and their behavioral profile, and number of individuals collected according to river basin (Jaguaribe = J, São Francisco = F and Coreaú = C).

Group	Species	Behavioral profile	J	F	C
1	<i>Astyanax bimaculatus</i> <i>Astyanax fasciatus</i> <i>Phenacogaster calverti</i> <i>Poecilia reticulata</i> <i>Poecilia</i> sp. <i>Serrapinnus heterodon</i> <i>Serrapinnus piaba</i>	Mostly small nektonic fishes feeding predominantly on insects in the water column or on the surface. They have no specific substrate preference and thrive in streams with low current flows.	441	767	1776
2	<i>Hoplias malabaricus</i> <i>Synbranchus marmoratus</i>	Piscivorous species, which ambush their prey. Nektonic or nektobentonic, they prefer streams with low current flows.	3	1	14
3	<i>Aspidoras menezesi</i> <i>Aspidoras rochai</i> <i>Aspidoras spilottus</i> <i>Corydoras garbei</i>	Small nektobentonic fishes, which sift through the substrate for food (usually aquatic invertebrates), preferably in faster-flowing streams.	14	67	119
4	<i>Hypostomus</i> sp. <i>Hypostomus jaguribensis</i> <i>Parotocinclus cearensis</i> <i>Parotocinclus haroldoi</i>	Benthic grazers feeding mostly on detritus. Most abundant in streams with riffles.	49	0	71
5	<i>Characidium bimaculatum</i> <i>Cichlasoma orientale</i> <i>Coptodon rendalli</i> <i>Crenicichla menezesi</i> <i>Rhamdia quelen</i> <i>Trachelyopterus galeatus</i> <i>Steindachnerina notonota</i>	Species with great trophic plasticity, feeding on plant debris, detritus, insects, and fish. Some stalk or pursue their prey, usually at twilight. The detritivore <i>S. notonota</i> is an exception.	14	64	64

#### Predictor variables

##### Phylogenetic history

To evaluate the evolutionary history of the humid forest enclaves in the Caatinga, a phylogenetic information matrix was built at the family level, exploring the descriptive aspect rather than the phylogenetic signs (Webb, 2000). Thus, following Sternberg & Kennard (2013), traits attributed to the phylogeny of the species were defined from a matrix of sampled streams (lines) vs. families (columns). For this, we built a matrix of species richness for each stream. Although phylogenetic predictors are often extracted using phylogenetic trees (Leibold et al., 2010), or palaeoecological differences between sampling locations (Castillo-Escrivà et al., 2017), we adopted Webb's classic approach due to the lack of detailed phylogenetic information for the endemic fauna of the study area, and also because the two humid forest enclaves displayed similar geology and formation history. Although their use may result in information loss, Ricotta et al. (2012) have demonstrated that cladistic relationships are strongly related to distance based on phylogenetic trees.

##### Spatial

A spatial predictor matrix was constructed using spatial analysis generating eigenvectors capable of capturing complex patterns in taxonomic and functional composition; eigenvectors with high eigenvalues are associated with large-scale spatial effects, while eigenvectors with low eigenvalues represent fine-scale effects (Griffith & Peres-Neto, 2006). We used asymmetric eigenvector maps (AEMs) to reflect the unidirectional flow of aquatic systems (Blanchet et al., 2008), at the hydrographic basin level (Declerck et al., 2011). Such eigenvectors are capable of modeling the distribution of species and functional groups within each basin but, to avoid bias related to the number of spatial predictors, only spatially structured vectors were selected (initially, 25) (Dray et al., 2012). To do so, Moran's  $I$  coefficients were calculated for each AEM, selecting those with significant spatial autocorrelation ( $p < 0.05$ ) (Blanchet et al., 2011). Subsequently, five eigenvectors representing large-scale forces were selected (AEM-1, AEM-2, AEM-3, AEM-4, AEM-6; Appendix 4).

#### *Environmental*

Using PCoA for the  $\log(x+1)$ -transformed data (except pH), the selected environmental variables were tested for redundancy. The purpose of the procedure was to identify variables with high collinearity in the PCoA biplot. After visual identification of obvious collinearities, we tested the variance of inflation (VIF) factor, excluding values  $>10$  from further analysis. The following variables were retained for the subsequent analyses: width, depth, elevation, temperature, pebble/gravel, coarse sand, fine sand, silt/clay and pH.

#### *Data analysis*

The importance of environmental (E), spatial (S) and phylogenetic (P; streams vs. family) components for taxonomic and functional structure was determined by partitioning the variance in a partial analysis of redundancy (pRDA), using Hellinger-transformed data (Borcard et al., 1992; Anderson & Gribble, 1998). Variables selected by forward selection were included in the pRDA as long as they did not exceed  $p=0.05$  (based on 999 Monte Carlo permutations). Previous selection of variables allows for a more reliable interpretation of the importance of the predictor variables.

Once the predictors were associated, the total variance was partitioned into eight components: (i) pure environmental (Ep), (ii) pure spatial (Sp), (iii) pure phylogenetic (Pp), (iv) spatially structured environmental (SE), (v) phylogenetically structured environmental (PE), (vi) spatially structured phylogenetic (SP), (vii) spatially and phylogenetically structured environmental (SPE), and (viii) unexplained (U). Following the recommendations of Peres-Neto et al. (2006), we estimated the adjusted coefficients of determination ( $R^2_{adj}$ ). Biplot ordinations were tested based on 10,000 permutations, assuming  $\alpha=0.05$ . Nestedness of the first axis of functional and taxonomic RDA (only for environmental variables) was determined with the nestedness overlap and decreasing fill (*NODF*) index (Almeida-Neto et al., 2008). We tested whether the observed *NODF* differed from the *NODF* derived from 1000 permutations of the species matrix of species and functional groups (SIM9 algorithm, Gotelli, 2000). We adopted this pattern based on the environmental conditions responsible for functional or taxonomic nestedness (observed *NODF* significantly different from expected *NODF*).

To control for biogeographical differences, an identity matrix was built for each hydrographic basin and used as covariable in a new partitioning analysis (PERMANOVA). Hydrographic basin level analysis suggested a homogeneous taxonomic (Pseudo- $F_{2,24}=1.01$ ;  $p > 0.38$ ), and functional (Pseudo- $F_{2,24}=1.07$ ;

$p > 0.35$ ), composition. The process consists of relating the predictive matrixes with the identity vector of the hydrographic basin of each stream in a residual environmental matrix ( $E_r$ ), and a residual phylogenetic matrix ( $P_r$ ). The identity of the hydrographic basin was controlled during the extraction of spatial eigenvectors (AEM). Finally, pRDA analyses were performed with the predictor matrixes  $E_r$ ,  $P_r$  and  $S$  and the response matrixes of species composition and functional groups, evaluating the influence of the hydrographic basin. All analyses were performed in R, version 3.4.2 (The R Foundation for Statistical Computing, 2017).

## Results

### *The forest enclave ichthyofauna*

Fish sampled comprised 23 species belonging to 5 orders and 11 families (Table S1.3 of Appendix 1). Siluriformes and Characiformes were the most strongly represented orders. Coreaú had the greatest number of species (17), followed by Jaguaribe and São Francisco (14 each). On average, 5.6 species (2-12) were captured per stream. Two of the registered species were non-native to the Caatinga. One of these, *Poecilia reticulata* Peters 1859, was widely distributed across samples sites, occurring in 69.2% of them. The most commonly captured native species was *Astyanax bimaculatus* (Linnaeus, 1758), occurring in 73.0% of the sites. Nektonic fish feeding on insects in the water column (Group 1) and ambushers with high trophic plasticity (Group 5) were the most species-rich and abundant groups in all basins (Table 2). In contrast, detritivorous and piscivorous species with strong substrate preferences had low abundances, occurring in specific environmental and elevational gradients. According to rarefaction procedures, the number of sites used ( $n = 26$ ) allowed complete sampling of the species richness of the study region (Figure S1 of Appendix 1).

### *Relative contribution of structuring factors (environment, space, and phylogeny)*

Following forward selection, three spatial eigenvectors (AEM-1, AEM-2 and AEM-4), phylogenetic information on the clades Characidae and Poeciliidae, and two environmental variables (elevation and channel width) (Table 3), together explained, respectively, 29% and 24% of the total variation in species composition and functional groups (Table 4). The components most important for the taxonomic approach were those spatially and phylogenetically structured by the environment (SPE) and the phylogenetically structured environmental (PE) (17% and 7%, respectively). In contrast, functional groups composition was explained primarily by the pure spatial component ( $Sp=13\%$ ;  $p=0.001$ ), followed by the pure phylogenetic component ( $Pp=7\%$ ;  $p=0.021$ ).

Table 3 Spatial, environmental, and phylogenetic predictors retained after forward selection for the taxonomic and functional approaches. The Cumulative  $R^2_{adj}$  (%) corresponds to the  $R^2_{adj}$  values of each variable within the RDA models which contain all the other variables. Statistically significant ( $p < 0.05$ ) variables, highlighted in bold, were retained.

Determinant	Variable	Taxonomic		Functional	
		Cumulative $R^2_{adj}$ (%)	$P$	Cumulative $R^2_{adj}$ (%)	$P$
Spatial	AEM-1	<b>17.4</b>	<b>0.02</b>	0.28	0.07
	AEM-2	<b>10.5</b>	<b>0.01</b>	29.7	0.21
	AEM-3	18.1	0.33	17.8	0.08

	AEM-4	17.7	0.31	<b>12.7</b>	<b>0.02</b>
	AEM-6	17.6	0.46	23.1	0.08
Environmental	Width	<b>15.7</b>	<b>0.01</b>	14.7	0.11
	Depth	16.2	0.85	11.6	0.60
	Elevation	<b>28.4</b>	<b>0.01</b>	<b>5.2</b>	<b>0.01</b>
	Temperature	29.2	0.14	18.1	0.16
	Pebble/gravel	31.8	0.59	9.8	0.12
	Coarse sand	32.4	0.06	7.1	0.91
	Fine sand	30.0	0.72	1.7	0.96
	Silt/clay	28.5	0.70	14.2	0.91
	pH	31.2	0.50	16.2	0.55
	Phylogenetic history	Auchenipteridae	29.3	0.08	18.8
Callichthyidae		31.3	0.37	12.9	0.26
Characidae		<b>19.3</b>	<b>0.01</b>	<b>8.6</b>	<b>0.04</b>
Cichlidae		30.2	0.64	18.7	0.34
Crenuchidae		26.0	0.13	10.4	0.83
Curimatidae		28.9	0.60	4.4	0.93
Erythrinidae		27.1	0.78	19.1	0.34
Heptapteridae		31.2	0.14	14.3	0.24
Loricariidae		21.4	0.90	12.1	0.15
Poeciliidae		<b>23.8</b>	<b>0.03</b>	18.6	0.13
Synbranchidae		24.6	0.80	15.1	0.72

The identity of the basins had little influence on taxonomic variation but was important for the functional groups (Table 4). For example, after controlling for basin identity, the phylogenetic component structured by the environment (PE=6%) and the pure phylogenetic component (Pp=5%;  $p=0.03$ ) explained most of the functional distribution (Table 4). Moreover, the pure environmental component increased in importance (Ep=3%,  $p=0.003$ ), while the pure spatial component decreased (Sp=2%;  $p=0.02$ ) when compared to the results of the analysis without controlling for hydrographic basin identity.

Table 4 Summary of results of variation partitioning of environmental, spatial, and phylogenetic history factors (%) on taxonomic and functional approaches with and without control for basin identity. Statistically significant components appear in bold ( $p<0.05$ ). Negative  $R^2_{adj}$  values are shown by <0 (see Table 3 for variables selected by forward selection). Ep=pure environmental; Sp=pure spatial; Pp=pure phylogenetic history; SE=spatially structured environmental; PE=phylogenetically structured environmental; SP=spatially structured phylogenetic; SPE=spatially and phylogenetically structured environmental; U=unexplained.

	Without basin identity control				With basin identity control			
	Taxonomic		Functional		Taxonomic		Functional	
	$R^2_{adj}$ (%)	$P$	$R^2_{adj}$ (%)	$P$	$R^2_{adj}$ (%)	$P$	$R^2_{adj}$ (%)	$P$
Ep	3	0.209	2	0.231	4	0.134	<b>3</b>	<b>0.003</b>
Sp	<0	0.403	<b>13</b>	<b>0.001</b>	1	0.326	<b>2</b>	<b>0.020</b>
Pp	1	0.279	<b>7</b>	<b>0.021</b>	2	0.220	<b>5</b>	<b>0.003</b>
SE	1	-	1	-	2	-	4	-
PE	7	-	2	-	5	-	6	-
SP	<0	-	<0	-	2	-	2	-
SPE	17	-	1	-	20	-	<0	-
U	71	-	76	-	80	-	80	-

A moderate proportion (28.8%) of the species distribution was explained by the environmental variables (Pseudo- $F=1.47$ ;  $p=0.03$ ), especially channel width and elevation (Table 3). The first RDA axis (11.7%) was formed by elevational gradient, with positive scores corresponding to narrow streams and negative scores to wide streams. Temperature (negative scores) and depth (positive scores) explained the second RDA axis (4.7%). Most species occurred in wider and moderately elevated streams (< 250 m a.s.l) (RDA axis 1; Figure 2a), without a nested distribution ( $NODF=48.11$ ;  $p=0.75$ ; Figure 3a). The distribution of functional groups was associated mainly with elevation (Figure 2b). Small species feeding mainly on small insects (Group 1), and carnivorous species (Group 2), occurred predominantly at intermediate to elevated altitudes (RDA axis 1; Figure 4), while small nektobenthic substrate-sifting species (Group 3), and benthic grazers feeding mostly on detritus (Group 4), predominated in wider streams with fine sandy substrates (intermediate elevation; Figure 4). Piscivorous and nocturnal species (Group 5) were markedly common in low elevations streams (< 200 m; Figure 4). These distribution patterns following the different elevational zones and explained the observed functional nesting patterns ( $NODF=76.23$ ;  $p=0.007$ ; Figure 3b).

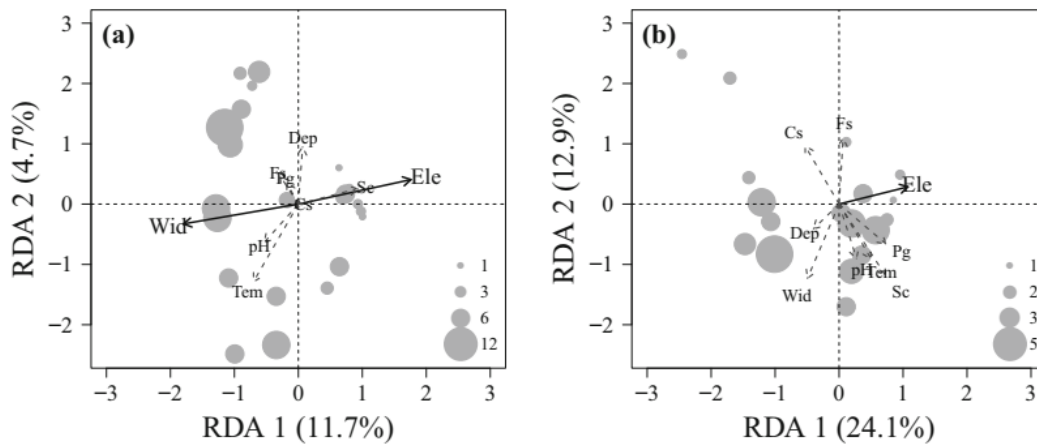


Figure 2 Ordination of 26 stream fish assemblages from forest enclaves in semiarid Brazil, based on the taxonomic structure (a) and functional groups (b). Loadings of significant and non-significant environmental determinants are represented by continuous and dashed arrows, respectively. The size of the circle represents the taxonomic richness and the functional groups in each sample unit.

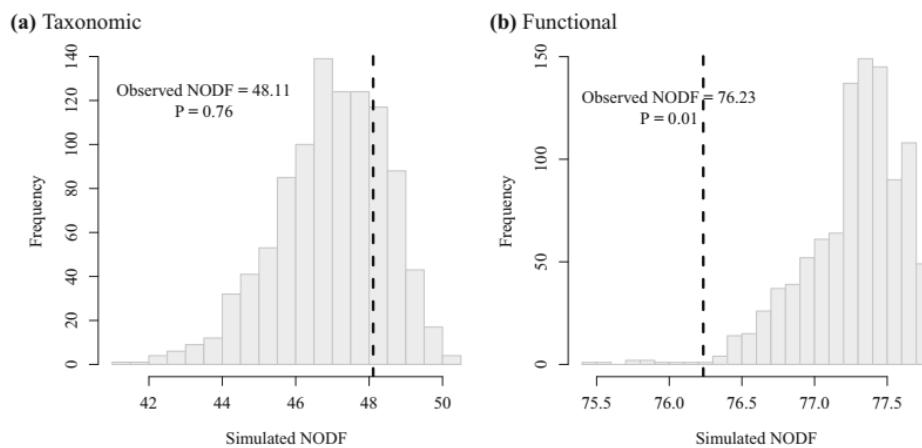


Figure 3 Simulated (bars) and observed (dashed line) values from the analysis of nestedness overlap and decreasing fill (*NODF*) for taxonomic (a) and functional (b) composition of stream fish assemblages from forest enclaves in semiarid Brazil. Dashed lines are *NODF* when rows of the incidence matrices were reordered following the first RDA axis (see Data Analysis in Methods section).

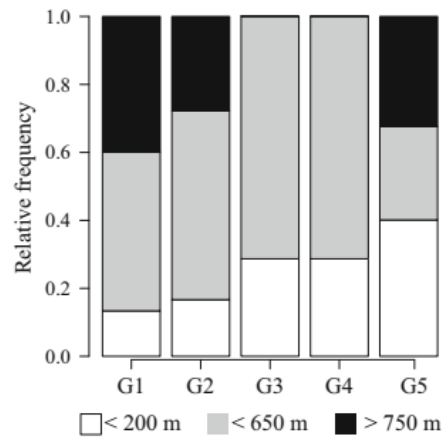


Figure 4 Relative frequency of individuals from each functional group of stream fish (G1 – G5) at each elevational zone from forest enclaves in semiarid Brazil. For details of each group, see Table 2.

## Discussion

Our study brings new information about community structure in headwaters, where niche-based processes are expected to predominate (Landeiro et al., 2011; Siqueira et al., 2012; Schmera et al., 2017; Zbinden & Matthews, 2017). By partitioning the variance of taxonomic structure, we separated the purely phylogenetic history (Pp) from the spatially and environmentally structured fish fauna. We demonstrated that the inclusion of phylogenetic history as a predictor can generate relevant information on the main factors structuring local communities. We also found that elevation gradients promote functional group nestedness, probably due to the differential dispersal capacity of species from different clades and environmental affinities. Taken together, our results help to clarify the relationship between historical and contemporary determinants in current patterns of fish biodiversity in headwater streams from semiarid Brazil.

### *Fish community assembly*

Recent studies on fish community have identified environmental variability (Ep, in this study) as the main component in explaining patterns of biodiversity (Cottenie, 2005; Peres-Neto et al., 2012; Sternberg et al., 2014; Viana et al., 2016; Bezerra et al., 2017). However, in our study, environmental conditions were not more important than the phylogenetically structured environmental component (PE). The importance of the phylogenetic history is reflected in the wide distribution of the clades Characidae and Poeciliidae, which may also be one of the explanations for the low importance of the spatial components in the taxonomic approach (spatial homogenization). Two major geological events were likely responsible for these findings in elevated streams in semiarid Brazil: marine incursions during Plio-Pleistocene in coastal areas, and the confluence of river systems resulting from subsequent headwater captures (Hubert & Renno, 2006; Dias et al., 2014). Headwater captures consists of connecting different river basins after a historical event (Dias et al., 2014). In the studied region, the geographic isolation of the three river basins

was interrupted 400,000 years ago when, after a glacial event, the course of the São Francisco River was modified, generating a dispersion corridor to the Jaguaribe and Coreaú river basins (Mabessone, 1994). Taken together, these historical events appear to be responsible for the similarity of the three basins in terms of the phylogenetic and spatial structure of their fish faunas. Based on the known history of the evolutionary radiation of the South American ichthyofauna (Lévêque et al., 2008), it was expected that species from the Characidae family would be very important in structuring local communities. However, the selection of the clade Poeciliidae (explained by the high occurrence of the introduced species *P. reticulata*) alerts us to the role of anthropic interventions in modifying the dynamics of local communities. Indeed, introduction of non-native species cannot be ruled out as a driver of taxonomic homogenization (Villéger et al., 2014). This becomes still more serious in view of the ability of such species to interfere directly in ecosystem functioning (Reznick, 1982).

Species composition was weakly explained by the identity of the hydrographic basin. Similar results were found by Heino et al. (2017), suggesting that spatial-environmental heterogeneity increases with increasing sampling scale. In fact, Rodrigues-Filho et al. (2016) found that the biotas of these two humid enclaves have similar species composition. However, variation in functional group composition was dependent on the biogeographic factor of the drainage basins. Therefore, we agree with Heino et al. (2017) that measuring biogeographical effects on local community variation is a difficult task. Thus, we suggest that further assessments should explore the main factors determining the composition of the functional groups after controlling for the hydrographic basin.

Pure components (Ep, Sp and Pp) in partitioning analyses should be interpreted with caution because the environmental gradients capable of influencing the community are difficult to quantify: variances are underestimated, whereas the spatial component is overestimated (Smith & Lundholm, 2010; Vellend et al., 2014). This problem has been documented mainly for environmental and spatial components, but it probably applies to other components as well (e.g. phylogenetic, biogeographical, connectivity). Nevertheless, our findings suggest the opposite pattern: large-scale spatial factors (AEM-4) and phylogenetic history were of greater importance in determining functional group composition. This may be due to functional differences in terms of dispersal capacity, associated with strong environmental selection and the complexity of the drainage network in headwater regions (Tonkin et al., 2018).

This result is not in agreement with the hypothesis of the drainage network position, which predicts greater importance for environmental conditions in headwater streams (Brown & Swan, 2010). This is indicated by the high importance of processes based on dispersion and phylogenetic history, reinforcing the emerging topic of context dependence in aquatic systems (Tonkin et al., 2016; Schmera et al., 2017). In fact, spatial structuring driven by dispersion (e.g., dispersion limitation and mass effect) has also been observed in headwater streams, to be an important structuring factor (Mykrä et al., 2007; Cetra et al., 2017). Thus, our results highlight the importance of combining environmental, spatial, and historical (SPE) factors when analyzing the factors shaping the structure of current local fish communities. While our results agree with the major community assembly theories, where phylogenetic history and spatial connectivity are key to selecting the regional species pool that will be filtered by local environmental conditions (Emerson & Gillespie, 2008), they are novel because they apply to communities of fish from headwaters of streams in a semi-arid area.



### *Nesting patterns in headwater streams*

As expected, species richness was greatest at intermediate altitudes and lowest in narrow and elevated streams (see Figure 2a). Wider streams generally offer more diversified habitats, an important feature in the structuring of fish communities (Mattos et al., 2014), and tend to be slightly warmer and deeper, so favoring greater species diversity (Ibanez et al., 2007; Báldi, 2008). However, the gradients of elevation and width do not show nested patterns in species composition. On the other hand, we observed nesting patterns for functional groups which could be the result of: 1) physical isolation preventing dispersal (Hill et al., 2017); 2) local communities being connected, but functional groups containing species with varying dispersal capacities (Thompson & Townsend, 2006; Heino, 2011, 2013), and 3) strong environmental gradients (Schmera et al., 2017). Based on the result of the partitioning analysis (while recognizing its limitations) and RDA, we believe the second and third options provide the most plausible explanation: the functional groups include species with varying dispersal capacities responding differently to the environmental gradient. Furthermore, the selection of eigenvectors with wide distribution (AEM-4) suggests dispersal limitation is more important than mass effect when explaining the local community structure within each basin (Heino et al., 2015).

Studies using functional traits to evaluate the influence of niche or dispersal-based processes in local communities usually classify fishes as either good and bad dispersers (e.g. Padial et al., 2014; Tolonen et al., 2018; but see Wojciechowski et al., 2017). Bad dispersers have spatially structured distribution, while good dispersers will spread as far as environmental conditions permit. In the current study, species were grouped canonically according to functional traits. We could thus explore functional traits responsible for the phylogenetic structure of fish communities, in line with habitat complexity (stream width/elevation relationship). Despite adopting a non-conventional functional approach to specifically explore the factors responsible for local fish community structure, our results also agree with those of studies that simply classified species into good and bad dispersers.

In river ecosystems, elevation gradients are well known for promoting species composition modifications in terms of habitat use, feeding, and locomotion (Jaramillo-Villa et al., 2010). In streams at lower altitudes (<200 m), nocturnal species that capture their prey by ambush were more strongly represented. These lowland streams were wider, favoring species with high maneuverability (e.g., Cichlidae), that rely on macrophytes for ambushing their prey (Ribeiro et al., 2016). At intermediate elevations (> 200 m and <650 m), streams were generally narrower, and substrate composed of pebble and gravel were more common. Here detritivorous and invertivorous species occurred in greater abundance. Species of these two groups show high fidelity to riffles habitats, and of then have low dispersal capacity (Pagotto et al., 2011). An abiotic and biotic transition occurs in streams located above 750 m, as there are smaller numbers of pools, fewer macrophytes and greater inputs of allochthonous material (C. A. S. Rodrigues-Filho, pers. obs.). In such streams, nektonic species that feed on small insects carried along by the stream are more commonly found. Due to their fusiform shape, these species have high dispersion capacity (Makrakis et al., 2010), which explains their often extensive distribution in streams at other altitudes. Similar patterns were observed by (Jaramillo-Villa et al., 2010), and reflect the adaptation of these species to highly hydrological complexity of headwater streams (Pusey et al., 2010). Lomolino et al. (2001) proposes that the modification of the diversity and species composition along

altitudinal gradients occurs because higher regions are more isolated. Such isolation, together with the low dispersion capacities and high environmental affinities of the species present in such regions promotes differentiation of functional composition, thus explaining the nesting patterns for the streams within the forest enclaves studied here. Indeed, similar results were reported by Taylor & Warren-Jr. (2001). According to these authors, extirpations of populations at higher altitudes promote significant nestedness at lower altitudes.

### *Conclusions*

We highlight the joint action of space, environment, and phylogenetic history in determining the fish community structure in the highlands of semiarid Brazil. Our results suggest that phylogenetic history is an important predictor of the community, acting together with environmental and spatial predictors to shape the distribution of species and functional groups of headwater streams. Specifically, we have confirmed that predictive models based solely on environmental conditions are not adequate to understand the functioning of metacommunities in headwaters. Thus, exploring the true reasons for the phylogenetic history of the study region and the dispersal capacity of the species become critical points for an understanding of the local dynamics of headwater fish communities (Eros et al., 2012). In addition, we have also shown that a basin's identity is important for the functional approach to community composition analysis, suggesting that idiosyncratic processes are more common than imagined in biological systems. This idiosyncrasy can be explained by the high hydrological variability of headwaters and the rapid response of the functional structure of communities to changes in the environment compared to the factors regulating taxonomic structure (Mouillot et al., 2013).

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## Supporting Information

### *Hydrobiologia*

#### How are local fish communities structured in Brazilian semiarid headwater streams?

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Appendix 1 Resume of biological and environmental data.

Table S1.1 List of sampling sites in high-altitude swamps located within the river basins of Jaguaribe (J), São Francisco (F) and Coreaú (C). Latitude and Longitude are expressed in decimal degrees.

Basin	Code	Name	Coordinates	Altitude (m)	Order
Jaguaribe	J1	Batateira	7°13'40''S 39°25'30''W	421	2
Jaguaribe	J2	Carrapato	7°13'51''S 39°25'30''W	421	1
Jaguaribe	J3	Constantino	7°16'01''S 39°23'36''W	528	1
Jaguaribe	J4	Currais	7°16'18''S 39°23'20''W	485	2
Jaguaribe	J5	Salamanca	7°19'41''S 39°21'26''W	432	3
Jaguaribe	J6	Seco	7°28'33''S 39°20'11''W	893	1
São Francisco	F1	Tabocas	7°26'11''S 39°50'10''W	625	1
São Francisco	F2	Cacimba	7°28'34''S 39°48'45''W	547	1
São Francisco	F3	Das Baixas	7° 29'00''S 39° 48'00''W	555	2
São Francisco	F4	São José	7° 27'00''S 39°44'00''W	787	2
São Francisco	F5	Brígida	7° 28'33''S 39°44'27''W	539	3
São Francisco	F6	[unnamed]	7° 47'13''S 39°24'31''W	519	3
Coreaú	C1	Rasgada	3°40'17''S 40°53'44''W	127	2
Coreaú	C2	Da Serra	3°42'09''S 40°51'53''W	156	2
Coreaú	C3	Passagem	3°22'55''S 41°06'03''W	112	2
Coreaú	C4	[unnamed]	3°22'07''S 41°06'23''W	111	1
Coreaú	C5	Pitimbú	3°15'08''S 41°07'09''W	65	2
Coreaú	C6	Gangorra	3°14'09''S 41°07'05''W	65	2
Coreaú	C7	Das Minas	3°50'00''S 40° 54'00''W	545	1
Coreaú	C8	Miranda	3°50'42''S 40° 54'59''W	840	1
Coreaú	C9	Gameleira	3°50'07''S 40°54'03''W	608	2
Coreaú	C10	Ubajara	3°49'32''S 40°53'30''W	419	3
Coreaú	C11	Cafundó	3°50'00''S 40°53'22''W	411	1
Coreaú	C12	Ubajara II	3°49'08''S 40°54'07''W	836	3
Coreaú	C13	Gavião	3°48'05''S 40°54'06''W	890	2
Coreaú	C14	Murimbeca	3°49'02''S 40°53'03''W	779	1

Table S1.2 Mean, minimum, maximum, and standard deviation (SD) of the variables. Water flow (m/s; Vel), flow rate (m; Wid), width (m; Dep), elevation (m; Alt), habitat volume (m<sup>3</sup>; Hvo), canopy cover (%; Can), temperature (°C; Tem), pH, dissolved oxygen (mg/L; OD), pebble/gravel (%; Pg), coarse sand (%; Cs), fine sand (%; Fs) and silt/clay (%; Sc), in the three drainage basins.

	Jaguaribe basin (n =6)			São Francisco basin (n = 6)			Coreaú basin (n =14)		
	Mean	Min-max	SD	Mean	Min-max	SD	Mean	Min-max	SD
Vel	0.39	0.2-0.6	0.15	0.51	0.4-0.9	0.13	0.22	0.1-0.4	0.09
Wid	6.80	3.5-8.7	2.89	8.12	6.6-10.6	2.33	4.10	1.1-8.0	1.80
Dep	0.18	0.1-0.4	0.11	0.10	0.0-0.2	0.06	0.19	0.0-0.3	0.08
Ele	536	421-893	167	610	539-778	104	468	65-890	323
Hvo	67.87	17.6-106.4	29.40	68.8	22.5-123.7	36.0	40.60	3.3-94.3	24.50
Can	0.48	0.1-0.8	0.27	0.65	0.4-0.8	0.15	0.33	0.0-0.6	0.20
Tem	23.40	22.0-25.0	0.88	27.04	26.9-27.3	0.15	25.19	21.0-29.0	2.18
pH	8.02	7.6-8.8	0.37	8.56	8.3-8.7	0.17	7.34	6.5-8.4	0.55
OD	9.04	7.5-10.1	0.77	12.16	11.9-12.5	0.23	9.85	2.4-13.0	2.69
Pg	12.58	0.0-57.4	20.51	33.38	0.4-89.4	37.37	25.12	3.0-58.6	17.89
Cs	5.50	1.3-12.4	4.23	11.20	2.7-20.7	7.27	13.25	2.4-32.4	7.45
Fs	77.99	30.0-95.9	23.07	54.32	4.6-91.1	37.50	53.28	20.4-87.0	20.10
Sc	3.91	0.5-11.0	3.42	1.29	0.0-4.5	1.87	8.35	0.4-33.3	8.89

Table S1.3 Presence (●) or absence (○) of species in humid forest enclaves in Northeastern Brazil, frequency of occurrence (%FO) in relation to the total number of specimens collected, and voucher numbers (Universidade Federal do Rio Grande do Norte/UFRN).

Species	Jaguaribe basin (J)						São Francisco basin (F)						Coreaú basin (C)								% FO	Vouchers						
	J1	J2	J3	J4	J5	J6	F1	F2	F3	F4	F5	F6	C1	C2	C3	C4	C5	C6	C7	C8			C9	C10	C11	C12	C13	C14
<i>Aspidoras rochai</i>	●	○	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	7.6	1879
<i>Aspidoras menezesi</i>	○	○	○	○	●	○	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	7.6	1521
<i>Aspidoras spilotus</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	●	●	○	●	●	●	○	○	23.0	1466
<i>Astyanax bimaculatus</i>	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	●	○	●	●	○	○	○	○	○	73.0	1195
<i>Astyanax fasciatus</i>	○	○	○	○	●	○	●	●	●	●	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	46.1	1879
<i>Characidium bimaculatum</i>	○	○	●	○	○	○	●	○	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	30.7	1320
<i>Cichlasoma orientale</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	●	●	○	●	○	○	○	○	○	○	○	○	○	19.2	361
<i>Coptodon rendalli</i>	○	○	○	○	○	○	●	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	7.6	2512
<i>Corydoras garbei</i>	○	○	○	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3.8	2685
<i>Crenicichla menezesi</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	15.3	943
<i>Hoplias malabaricus</i>	○	○	●	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	15.3	1261
<i>Hypostomus</i> sp.	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	7.6	3221
<i>Parotocinclus cearensis</i>	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	34.6	1505
<i>Parotocinclus haroldoi</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	19.2	1294
<i>Phenacogaster calverti</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3.8	2511
<i>Poecilia</i> sp.	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3.8	1468
<i>Poecilia reticulata</i>	●	○	●	●	○	●	○	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	69.2	1476
<i>Rhamdia quelen</i>	●	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	11.5	1201
<i>Serrapinnus heterodon</i>	○	●	●	○	●	○	●	○	○	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	46.1	1677
<i>Serrapinnus piaba</i>	○	○	○	○	●	○	●	○	○	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	26.9	2677
<i>Steindachnerina notonota</i>	○	○	○	○	●	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	26.9	1884
<i>Symbranchus marmoratus</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	19.2	3226
<i>Trachelyopterus galeatus</i>	○	○	○	○	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	3.8	-

The identification of the species was based on, Lui et al. (2010), Ferraris (1999), Britto (2000), Oyakawa and Mattox (2009), Kullander and Lucena (2006), Garavello (1976) and by consultation to specialists in fish taxonomy of the Brazilian semi-arid.

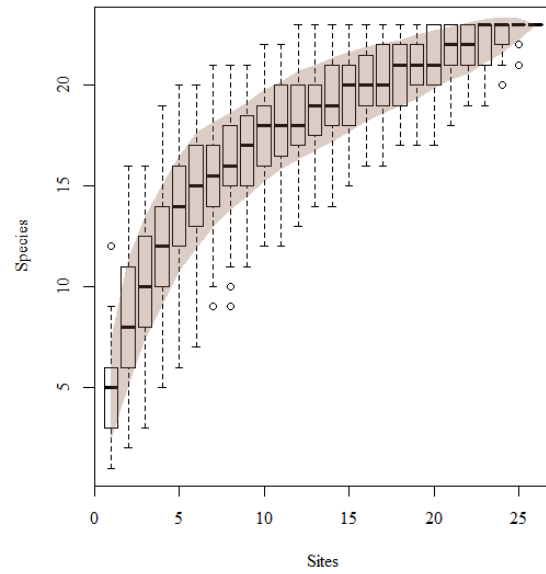
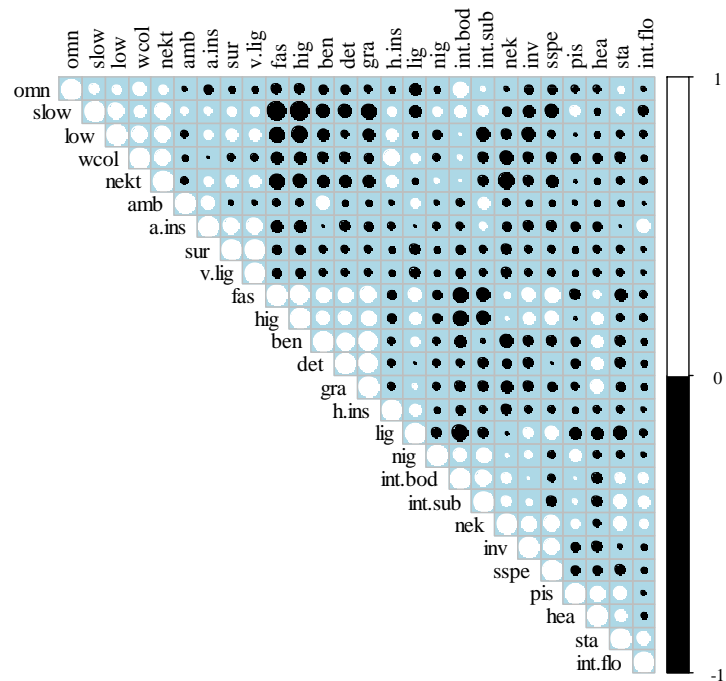


Figure S2 Accumulation curve of the 26 headwater streams, sampled in the Jaguaribe, Coreaú and São Francisco River basins

Appendix 2 Positive (white) and negative (black) Pearson correlations between functional traits of species. See Table 1 for abbreviations. The functional traits represented different facets of functional structure ( $r < 0.7$ ).



## Appendix 3 Resume of functional analysis.

Table S3.1 Functional traits of species sampled in headwaters in the Coreau, Jaguaribe and São Francisco River basins, Brazil.

Family	Species	Functional traits					
		Diet	Feeding tactic	Vertical compartment	Current flow	Body mass	Specify for substrate
Auchenipteridae	<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	Invertivore	Night active	Nektobenthic	Low	Intermediate	Intermediate
Callichthyidae	<i>Aspidoras menezesi</i> Nijssen & Isbrücker, 1976	Invertivore	Speculation	Nektonic	Fast	Light	High
Callichthyidae	<i>Aspidoras rochai</i> Ihering, 1907	Invertivore	Speculation	Nektonic	Fast	Light	High
Callichthyidae	<i>Aspidoras pilotus</i> Nijssen & Isbrücker, 1976	Invertivore	Speculation	Nektonic	Fast	Light	High
Callichthyidae	<i>Corydoras garbei</i> Ihering, 1911	Invertivore	Speculation	Nektonic	Fast	Light	High
Characidae	<i>Astyanax bimaculatus</i> (Linnaeus, 1758)	Omnivore	Water column	Nektobenthic	Slow	Intermediate	Low
Characidae	<i>Astyanax fasciatus</i> (Cuvier, 1819)	Omnivore	Water column	Nektobenthic	Slow	Intermediate	Low
Characidae	<i>Phenacogaster calverti</i> (Fowler, 1941)	Aquatic insectivore	Water column	Nektonic	Slow	Light	Low
Characidae	<i>Serrapinnus heterodon</i> (Eigenmann, 1915)	Herbivorous insectivore	Water column	Nektobenthic	Slow	Light	Low
Characidae	<i>Serrapinnus piaba</i> (Lütken, 1875)	Herbivorous insectivore	Water column	Nektobenthic	Slow	Light	Low
Cichlidae	<i>Cichlasoma orientale</i> Kullander, 1983	Invertivore	Stalker	Nektobenthic	Slow	Intermediate	intermediate
Cichlidae	<i>Crenicichla menezesi</i> Ploeg, 1991	Aquatic insectivore	Stalker	Nektonic	Intermediate	Intermediate	Intermediate
Cichlidae	<i>Coptodon rendalli</i> (Boulenger 1897)	Omnivore	Stalker	Nektonic	Slow	Intermediate	Intermediate
Crenuchidae	<i>Characidium bimaculatum</i> Fowler, 1941	Aquatic insectivore	Ambusher	Nektobenthic	Slow	Light	Intermediate
Curimatidae	<i>Steindachnerina notonota</i> (Miranda-Ribeiro, 1937)	Detritivore	Filterer	Nektonic	Slow	Intermediate	Low
Erythrinidae	<i>Hoplias malabaricus</i> (Bloch, 1794)	Piscivore	Stalker	Nektonic	Slow	Heavy	Intermediate
Heptapteridae	<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	Piscivore	Night active	Nektonic	Slow	Intermediate	Intermediate
Loricariidae	<i>Hypostomus</i> sp.	Detritivore	Grazer	Benthic	Fast	Heavy	High
Loricariidae	<i>Parotocinclus cearensis</i> Garavello, 1977	Detritivore	Grazer	Benthic	Fast	Light	High
Loricariidae	<i>Parotocinclus haroldoi</i> Garavello, 1988	Detritivore	Grazer	Benthic	Fast	Light	High
Poeciliidae	<i>Poecilia reticulata</i> Peters, 1859	Aquatic insectivore	Surface	Nektobenthic	Slow	Very light	Low
Poeciliidae	<i>Poecilia</i> sp.	Aquatic insectivore	Surface	Nektobenthic	Slow	Very light	Low
Synbranchidae	<i>Synbranchus marmoratus</i> Bloch, 1785	Piscivore	Stalker	Nektobenthic	Slow	Heavy	High

Table S3.2 Eigenvalues, % explanation, % cumulative explanation, and broken-stick values of principal coordinates analysis (PCoA). Only the first eight axes presented eigenvalues higher than the broken-stick values and were retained for the determination of the functional groups.

Axis	Eigenvalues	% Explanation	% Cumulative explanation	Broken-Stick
PCoA1	3.164	0.252	0.252	0.167
PCoA2	1.651	0.142	0.395	0.122
PCoA3	0.879	0.086	0.482	0.099
PCoA4	0.630	0.068	0.550	0.084
PCoA5	0.423	0.053	0.603	0.073
PCoA6	0.259	0.041	0.645	0.063
PCoA7	0.243	0.040	0.685	0.056
PCoA8	0.124	0.031	0.717	0.049
PCoA9	0.036	0.025	0.742	0.044
PCoA10	0.000	0.022	0.765	0.039

Table S3.3 Scores of traits categories in the two axis of PCoA.

Traits categories	PCoA1	PCoA2
Aquatic insectivore	0.2333	-0.1066
Herbivorous insectivore	0.2418	-0.3532
Invertivore	-0.2163	0.2032
Omnivore	0.3801	0.0350
Piscivore	0.1584	0.1482
Water column	0.3269	-0.2678
Substrate filterer	-0.3040	0.1595
Ambusher	0.0093	-0.0748
Grazer	-0.5482	-0.1876
Night active	0.2555	0.2836
Stalker	0.1599	0.2749
Surface	0.3792	-0.2877
Benthic	-0.4367	-0.1650
Nektonic	-0.0550	0.2643
Nektobenthic	0.3037	-0.2019
Reduced biomass	0.3792	-0.2877
Low biomass	-0.2113	-0.1001
Medium biomass	0.2718	0.2271
Big biomass	-0.2050	-0.0601
Low flow rate	0.2536	-0.0187
Intermediate flow rate	0.1346	0.4540
High flow rate	-0.4923	-0.0217
Low preference	0.3123	-0.1741
Moderate preference	0.1786	0.3028
High preference	-0.4313	-0.0278

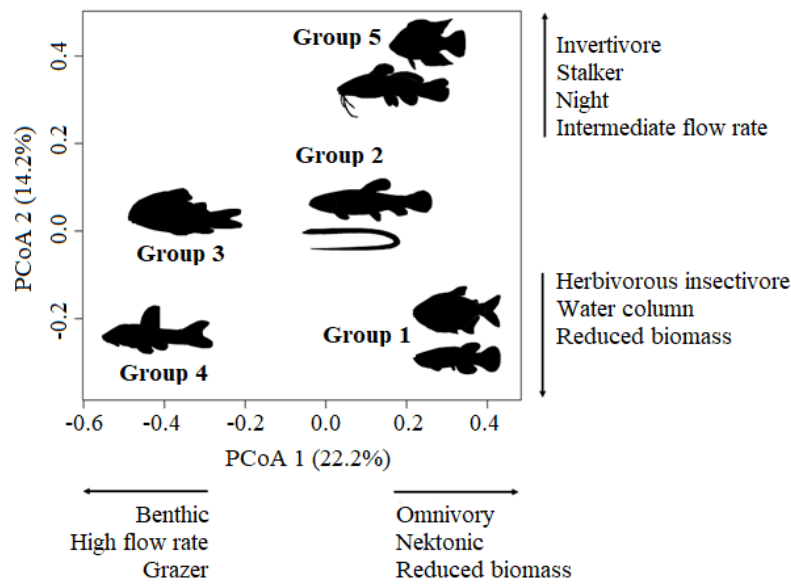
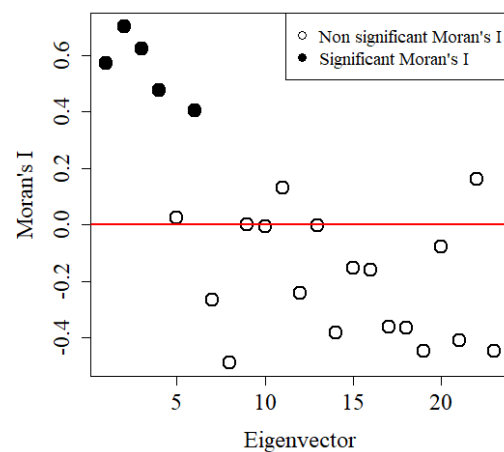


Figure S3 Mean position of the functional groups in the bi-dimensional space of the PCoA. The figures represent the general format of the species within each group. Look at table 2 for the complete list of species in each group.

Appendix 4 Moran's  $I$  for 25 asymmetric eigenvectors maps (AEM). Black points above the red line represent the eigenvectors that have a positive spatial correlation. Red line represents the expected value under null hypothesis.



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**CAPÍTULO 2**

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**OECOLOGIA****COMMUNITY ECOLOGY – ORIGINAL RESEARCH**

Title: Historical and ecological drivers of community assembly of the Amazonian stream fish assemblages

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**Abstract**

There is a paucity of empirical research and a lack of predictive models considering the interplay between the influence of historical and ecological processes on community assembly. A bridge that connects predictive models and community assembly could be assessed by considering a trait-based approach that arrays species and functional traits that respond to changes in eco-evolutionary gradients. In this context, we investigated the importance of historical and ecological drivers in explaining the trait distribution of stream fish assemblages from the Brazilian Amazonia across twenty-one sub-basins. To do that, we first built a custom-null model considering dispersal limitation to evaluate whether observed trait distribution is lower (underdispersion) or greater (overdispersion) than expected. Using the Kolmogorov test, we found an overall tendency for trait overdispersion of fish assemblages, which we interpret to be a result of the relative hydrological stability of the Amazon Basin. Then, using linear mixed models (LMM), we found that marine incursions (~5 Mya) created assemblages with trait underdispersion patterns. Similar trait patterns were observed for assemblages inhabiting streams with high current velocity. Together, this result suggests that historical and ecological drivers can create similar trait patterns. Conversely, streams embedded in basins with low productivity and low pH (black waters) present a tendency for trait overdispersion. Our results point to the importance of considering historical and ecological drivers in understanding the trait distribution patterns in local assemblages.

**Keywords:** Functional biogeography · Species pool · Trait underdispersion · Trait overdispersion · Null models

## Introduction

The species distribution across space and time are recognized to be the result of the interplay between historical and ecological processes. The first act predominantly at larger spatial and temporal scales, defining regional species pool (e.g., a set of species in a region able to colonize local communities), while the latter act mostly at smaller scales, defining more fine-tuned properties of the local communities (Vellend 2016; Rapacciuolo and Blois 2019). This notion has fueled the idea that the structure of local communities reflects the predominant outcome of ecological processes (Weiher and Keddy 1995), while historical processes has been often ignored in studies focusing on the community assembly (Münkemüller et al. 2020). However, long-standing evidence shows that this simplistic view is fraught with many exceptions in nature (Chase 2003; Johnson and Stinchcombe 2007; Medina et al. 2018). Thus, understanding how historical and ecological processes interact to define local communities is at the forefront of the debate on processes underlying community assembly.

Many of our ideas on predictable mechanisms underlying community assembly are based on the premise that species differ in their ecological requirements for survival and growth through different filters (Cornwell and Ackerly 2009; Weiher et al. 2011). In this context, a deterministic view of community assembly state that local communities are composed by species capable of reaching them (i.e., overcome dispersal filter) and having combinations of functional traits (e.g., morphology, physiology, behavior) that favor their local establishment under certain circumstances (i.e., environmental conditions and species interactions) (de Bello et al. 2012). At broad spatial scales, speciation, extinction, or colonization history act as filters defining the regional trait profiles available to occur in local communities (Mittelbach and Schemske 2015; Pinho et al. 2021). For instance, certain functional traits are more likely to be absent in regions that have been experienced long-term extinctions and posterior colonization, whereas high speciation levels and relative historically stability led to a broad regional trait diversity (Cilleros et al. 2016; Hagge et al. 2019). Species assemblages colonized from a less diverse species pool would thus have narrower trait diversity than expected (i.e., a pattern namely trait underdispersion) when compared to species assemblages colonized from a high-diverse species pool that would be more likely to present greater trait diversity than expected (i.e., trait overdispersion). These predictions assume that the regional diversity of functional traits influences the local community structure, which can be plausibly expected from theoretical (Spasojevic et al. 2018) and empirical studies (Patrick and Brown 2018). In addition, trait underdispersion and overdispersion can be observed when habitat conditions favor species with a particular suite of traits to coexist (i.e., species with similar traits) or when high productivity makes possible functionally different species to coexist (i.e., species with distinct traits), respectively (Chesson 2000). Therefore, assessing changes in trait patterns in communities along eco-evolutionary gradients can shed light on the identification of the main processes underlying community assembly.

One of the main challenges to understanding the assembly of local communities considering the multiple spatial-temporal scales under a functional perspective is the need to have a dataset encompassing regions with different evolutionary histories coupled with local abiotic (e.g., local habitats) and biotic information (e.g., species abundance, composition, and trait characteristics). In this context, fish

assemblages inhabiting headwater streams in Amazonia are an excellent model system. First, stream fish are often isolated within drainage basins, highlighting the importance of particular historical events enclosed within clear biogeographical delimitations. Second, these assemblages are structured by abiotic conditions acting in multiple scales that differ between sub-basins (Santos et al. 2019; Benone et al. 2020). Third, there are many stream ecosystems throughout Amazon River basins with quite different local habitats and evolved under different evolutionary histories (Mendonça et al. 2005).

Amazonia River basins have passed through several historical events since Paleogene (~65 Mya; Hoorn *et al.*, 2010). Western and Eastern Amazonian regions were isolated from each other for ~55 million years, being connected only during the mid to late Miocene (~9 to 5 Mya) (Hoorn et al., 2010). During this isolation period, the two regions experienced different intensities and frequencies of historical events. For example, a large and shallow wetland lake system (i.e., the Pebas Lake system) in the Western Amazonia provided new aquatic stable environments for freshwater biota (Wesselingh 2006). The Pebas system became fluvial and flowed eastward during the mid-late Miocene (Latrubesse et al. 2010). On the other hand, Eastern regions have experienced long marine incursions (~5 Mya, with a duration of ~ 0.8 My), severely reducing freshwater environments and extinguishing a vast portion of their associated diversity (Fontenelle et al. 2021). This historical scenario has been assumed to shape the Amazonian ichthyofauna (Oberdorff et al. 2019), and thus we believe that it might also be critical in shaping the functional trait patterns of local stream fish assemblages. For example, marine incursions may have restricted the regional range of fish traits in Eastern regions available to occur in local assemblages, leading to a functional pattern of trait underdispersion compared to assemblages that have not been submerged by the sea. On the other hand, high speciation and relative historical stability provided by the Pebas system might enhance the morphological and trophic specialization of fish species, enabling them to finely partition resources (e.g., Nicholson and Clements 2021). Local assemblages should thus be composed of species with a set of very distinct functional traits (i.e., trait overdispersion) when compared to assemblages that have not been connected to the Pebas lake system.

Properties of River basins and local habitat conditions strongly influence the stream fish assemblages in Amazonia (Benone et al. 2020; Bogotá-Gregory et al. 2020). Thus, the stream fish's trait composition and diversity also vary among sites in response to chemical and physical conditions predominantly found within the hydrological basin (Rodrigues-Filho et al. 2017; Bower and Winemiller 2019a). Amazon rivers can be divided into three predominant watercolors (i.e., white, clear, and black) with different chemical and physical conditions that are supposed to prevent fish dispersal throughout river basins (Bogotá-Gregory et al. 2020). White waters mostly have an Andean origin and a high concentration of sediments, enhancing the basin productivity, while clear and black waters have lower productivity. The high productivity might allow more species with different traits to coexist, thereby creating diverse fish assemblages (Mudrák et al. 2016). On the other hand, the black-water systems are characterized by low productivity and very acid waters, representing a strong chemical filter for fishes (Dangles et al. 2004). This filter might restrict the occurrence of species with particular traits resulting in less diverse fish assemblages (Weiher and Keddy 1995). Instream habitat conditions are also considered an essential driver of the functional structure of Amazonian stream fishes (Leitão et al. 2018). For instance, Amazonian streams are typically characterized by the substrate composed of sand and litter with

low current velocity (Mendonça et al. 2005). These conditions can be assumed to relax the filter to fish morphology by minimizing the energetic cost to play basic behaviors (Gatz 1979), which would create an overdispersion pattern of traits within fish assemblages. Streams with characteristics that depart from this typical physical structure (e.g., rocky substrate and high-current velocity) should thus impose a strong filter to fish species, which would create an underdispersion pattern of functional traits. Amazonian streams can therefore be arrayed along an environmental gradient uniqueness. The greater the environmental uniqueness (i.e., instream conditions far from the typically found across the Basin), the greater the tendency of trait underdispersion patterns.

**Table 1** Assumptions and hypotheses derived from community assembly theory, associated with the relative importance of historical and ecological processes in explaining the patterns of functional trait diversity (i.e., under or overdispersion) within local stream fish assemblages in the Amazon Basin.

Process/Driver	Assumptions	Hypotheses
<b>Historical</b>		
Pebas connection	High speciation increases the range of traits at the regional scale available to reach local habitats <sup>1</sup>	Assemblages historically connected to the Pebas lake system present greater functional diversity than expected by chance (i.e., trait overdispersion) in comparison to assemblages never connected
Marine incursions	Extinctions decrease the range of traits at the regional scale available to reach local habitats <sup>1</sup>	Streams that have been submerged by marine incursions ~5 Mya present lower functional diversity than expected by chance (i.e., trait underdispersion) in comparison to those that have not been submerged
Distance to the Amazon River mouth	Regions colonized later should have a lower range of traits available to reach local habitats <sup>1</sup>	Latter colonization of Eastern basins resulted in decreased functional diversity in their local assemblages than expected (i.e., trait underdispersion) compared to the assemblages of the Western basins
<b>Ecological</b>		
Watercolors [white, clear, and black]	High productive basins favor more species with different functional traits to coexist <sup>2</sup>	Assemblages located in white-water basins have higher functional diversity than expected (i.e., trait overdispersion) when compared to assemblages located in black and clear-water basins
Environmental uniqueness	Unique environmental conditions favor a particular suite of traits values, allowing only a few species and with more similar traits to coexist <sup>2</sup>	Streams with habitat conditions more divergent from the typical conditions found in the Amazon Basin have assemblages with lower functional diversity than expected by chance (i.e., trait underdispersion) when compared to streams with typical conditions

<sup>1</sup>Spasojevic et al. (2018); <sup>2</sup>Weiherr and Keddy (1995)

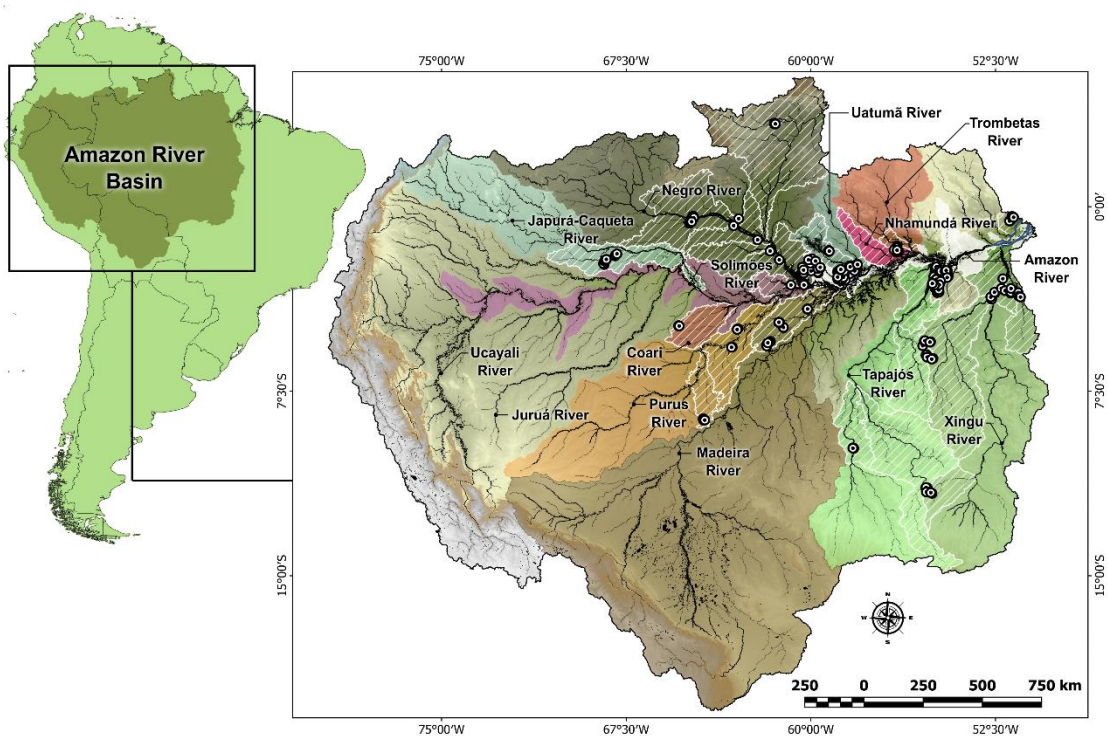
Here, we investigated the importance of historical and ecological drivers to the functional structure of fish assemblages from 305 streams distributed across 21 sub-basins in Amazonia. To do that, we conducted an analytical protocol assuming that species are not free to disperse through all sub-basins (i.e., dispersal filter) to specifically test for the contrasting patterns of functional trait diversity within assemblages (i.e., trait under versus overdispersion). Precisely, we assess: 1) if Amazonia stream fish assemblages have a major pattern of functional trait underdispersion or overdispersion; and 2) which historical and ecological processes have driven these opposing patterns. We expect that the trait

underdispersion and trait overdispersion pattern will change along with the historical and ecological variation (Table 1).

## Materials and methods

### *Sub-basin delimitation and data sampling*

The study was based on a fish inventory of 305 headwater streams sampled across hydrological sub-basins of the Amazon River Basin, covering more than 2 million km<sup>2</sup> (Figure 1). The sub-basins were delimited by Oberdorff et al. (2019), which found a marked taxonomic difference between them, indicating that this delimitation captures the general taxonomic distribution patterns in Amazonia rivers. Specifically, the sub-basins were extracted from the HydroBASINS framework ([www.hydrosheds.org/page/hydrobasins](http://www.hydrosheds.org/page/hydrobasins)), a subset of the HydroSHEDS database (Lehner and Grill 2013). The levels 5 and 6 were combined with a constraint area of > 20,000 km<sup>2</sup> to build the sub-basins (Jézéquel et al. 2020). Sub-basins with few streams sampled ( $n < 3$ ) were excluded from our analyses. After that, we obtained a dataset with 288 streams belonging to 21 sub-basins. Importantly, although excluded streams did not compose statistical analyses, their information was used to delimitate regional species pools (see below).



**Figure 1** Geographic locations of sampled stream fish assemblages in the Brazilian Amazon (305 points represented by white dots). Sub-basins (white dashed area) are delimited based on HydroBASINS. The major tributaries of the Amazon Basin are represented in distinct colors.

Streams were sampled in pristine regions covered primarily by dense *terra firme* rainforest. The hydrological regime is considered stable over time, where local rains are responsible to influences fishes' taxonomic and functional composition (Espírito-Santo et al. 2013; Borba et al. 2021). During heavy rain



events, temporary pools are formed laterally to streams providing shelter for many fish species. These pools are responsible to maintain the fish population relatively stable throughout the year (Espírito-Santo and Zuanon 2017). However, exceptions for this general pattern are observed in some sub-basins such as the Purus-Madeira interfluvial, where streams have an intermittent dynamic (Stegmann et al. 2019). The samples were carried out between 2001 and 2016 following the standard protocol of Mendonça et al. (2005). We measured local environmental conditions in each stream site (50-m long stretch), including channel depth and width, current velocity, and substrate composition. All sampling sites are located at altitudes from near zero to 300 m a.s.l. Stream depth (m) and width (m) were measured with a ruler and measuring tape, and velocity (m/s) was estimated by the time necessary for a floating object to cover a known linear distance along the main channel. The relative substrate composition (%) was estimated based on the frequency of occurrence of eight distinct categories: clay (0.01-0.1 mm), sand (0.1-1 mm), pebble/gravel (1-110 mm), fine litter (fine organic matter), coarse litter (dead leaves), roots of the riparian vegetation, trunk (diameter > 10 cm), and aquatic plants.

After environmental characterization, fishes were caught during daylight hours with sieve and seine nets, euthanized by immersion in an anesthetic solution of Eugenol, fixed in 10% formalin, and then preserved in 70% alcohol. Voucher specimens are deposited in the Fish Collection of the National Institute for Amazonian Research (INPA, Manaus). Overall, we caught 48 495 fish individuals belonging to 375 fish species, 36 families, and nine orders and the streams supported an average of 13 species (standard deviation = 8.47) and 155 individuals (standard deviation = 160).

#### *Functional structure of fish assemblages*

To describe the functional structure of the fish assemblages we conducted an ecomorphological analysis based on a set of morphometric data collected from 3-10 adult individuals of each species. Combinations of these measures generated eighteen functional traits related to locomotion capacity, food acquisition, and water-column occupation (for details, see Appendix S2 in Supporting Information). Some functional traits (e.g., teeth type) were not coded as quantitative variables; thus, we used the Gower distance to quantify the functional distance among species pairs (Pavoine et al. 2009). We then conducted a principal coordinate analysis (PCoA) on the Gower dissimilarity matrix to build a multidimensional functional space from which the functional structure of local assemblages was estimated (Figure S2.2). Based on the protocol developed by Maire et al. (2015) to determine the number of axes that guarantee a high-quality functional space, we used the first five PCoA axes (Figure S2.2).

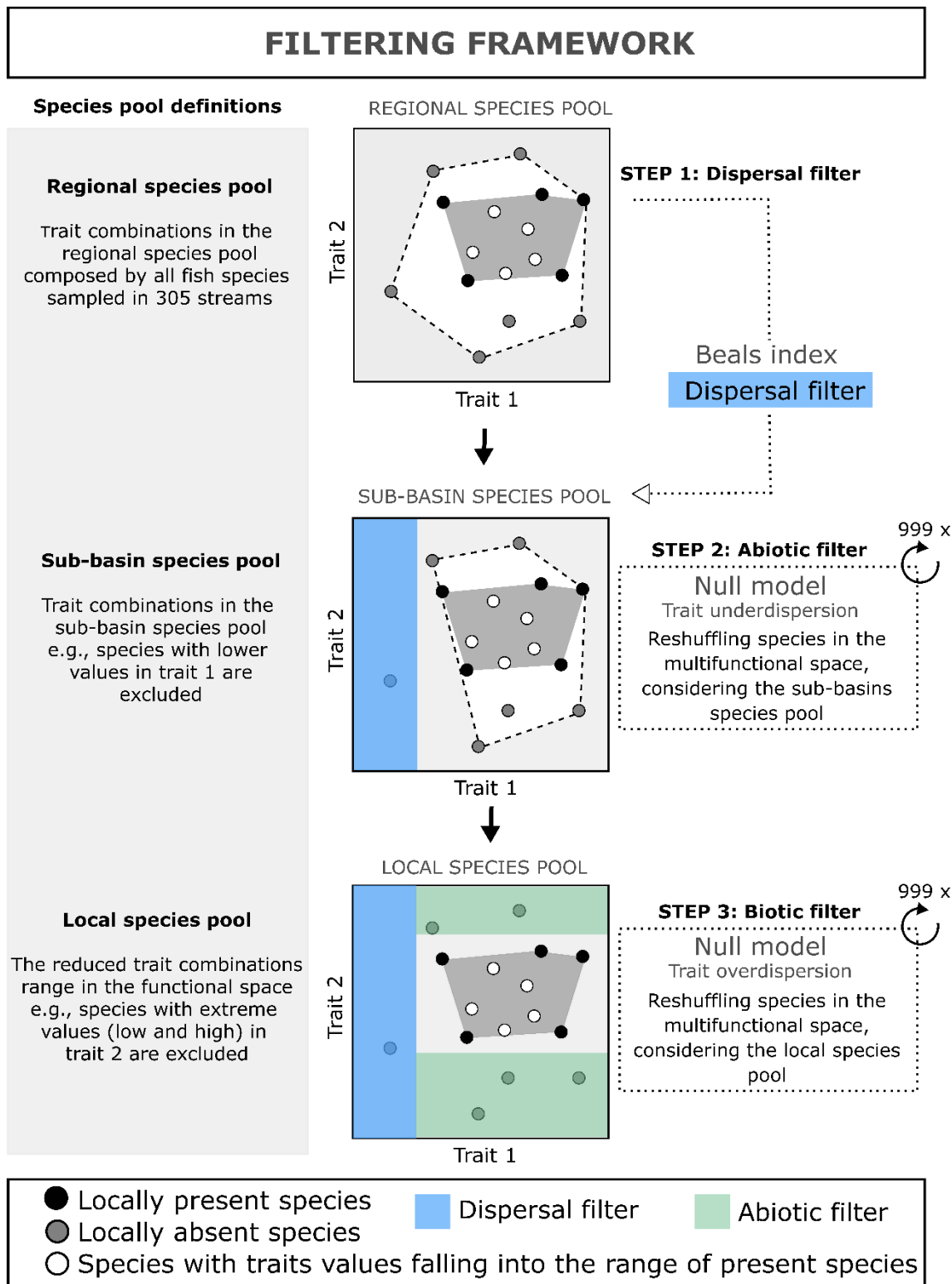
We computed two indices to describe the functional diversity of each fish assemblage: functional dispersion (FDis); and functional distinctiveness ( $D_i$ ). FDis describes the spread in functional traits among species in a given community; it is expressed by the mean distances of each species, weighted by its abundance, from the community centroid in the functional space (Laliberté and Legendre 2010). FDis is low when species are close and high when species are distant from the community centroid. The functional distinctiveness ( $D_i$ ) measures the mean distance of each species from the other species within a given community, weighted by their differences in abundance (Violle et al. 2017). Species showing trait combinations similar to the rest of species in a given community will have low  $D_i$ , while species showing

unique trait combinations will have high  $D_i$ . To scale up this species-level information to the community level, we calculated the mean value of  $D_i$  for each fish assemblage (i.e., the community functional distinctiveness, herein  $FD_i$ ). These two indices capture complementary information about the community structure related to trait overdispersion and trait underdispersion (Botta-Dukát and Czúcz 2016).

*Conceptual framework: Assessing trait under and overdispersion*

We used null models and compare observed values of functional dispersion ( $FD_i$ ) and functional distinctiveness ( $FD_i$ ) against those expected by chance to detect the pattern of trait distribution within fish assemblages. An important point that must be considered in community assembly studies is that different patterns can be observed at different scales (de Bello et al. 2012). For example, while abiotic filters prevent species establishment from a broader species pool, biotic interactions become more important on a scale where abiotic filters have already selected a subset of species from the species pool. Consequently, null models should accommodate these scale differences to provide more reliable inferences about community assembly patterns (e.g., trait underdispersion or trait overdispersion).

Hence, we adopt a hierarchical framework in which the community assembly results from subsequent filters (Figure 2). This framework assumes that species are not present everywhere, even when local conditions are suitable for them. For example, even if a given fish species can establish and persist in streams with high current velocity, they should not colonize all Amazonia streams with this characteristic because dispersal limitations prevent it. Therefore, although we sampled 375 fish species, not all of them should be part of the species pool used to construct random communities with the null models. The simplest way to deal with this is to use the inventory of species caught within sub-basins. However, this approach ignores geographical constraints that limit species dispersion (Lewis et al. 2016). To deal with this, we estimated the species pool composition of the 21 sub-basins in which streams are distributed (step 1 in Figure 2) using species co-occurrence patterns. In this approach, a species that is absent from a given sub-basin is considered to be a part of the species pool if usually co-occurs with species present in this sub-basin. Thus, we calculated a co-occurrence probability which calculated the probability of species occurrence based on the co-occurrence of a given species with others, using the Beals index (Beals 1984). Then, the co-occurrence probability for each species was used to define whether it should be included in the pool of any given sub-basin, assuming a threshold of 5%. In practice, the Beals index estimates the composition of the species pool for each sub-basins considering biogeographical factors that limit the dispersion of a given fish species between far river basins (e.g., between Madeira and Japurá Rivers; Figure 1). Thus, our species pool estimation considers that major Amazon River tributaries act as a barrier to fish dispersion, which has been supported by cellular automata analysis (Santorelli et al. 2022).



**Figure 2** The filtering framework applied to assess the trait assembly patterns in the Amazonian stream fish assemblages. The functional space built with two hypothetical traits for the regional species pool is shown at the top, followed by dispersal, abiotic and biotic filters that take out species along the process of local community assembly. The filtering framework is conceived in three steps. Step 1: Determine which species can potentially disperse to local communities within a given sub-basin, creating the sub-basin species pool. Step 2: Species from the sub-basin species pool are dispersed to the local habitat, and abiotic

filters exclude those with unfit traits combinations, creating the local pool. Step 3: Biotic interactions determine which species can coexist within the local pool. Null models were applied in steps 2 and 3 to test for the trait underdispersion and overdispersion, respectively.

Using the composition of the sub-basin species pool, we built a null model to initially test for the effect of environmental filtering with a consequent pattern of trait underdispersion within assemblages (step 2 in Figure 2). To do that, we reshuffled the species position in the multifunctional space (i.e., species names in PCoA scores matrix) according to the continuous differences in species abundance (i.e., reshuffling between two species with similar abundance is much more likely than between species with highly different abundances) to prevent that rare trait combinations become common during randomizations (Wilson and Stubbs 2012). In this randomization, both species richness in the local fish assemblages and species frequency across assemblages were fixed. For example, let us imagine a given local community with ten species embedded in a sub-basin with a pool of one hundred species. In this case, the null model reshuffled ten out of one hundred species (without replacement), considering their abundances.

In the next step, to test for the trait overdispersion, it is important initially to control for trait underdispersion as much as possible (Bernard-Verdier et al. 2012). So, we only included in the species pool composition those species that potentially tolerate similar abiotic conditions with those locally found (hereafter local species pool; step 3 in Figure 2). The local species pool composition represents all species in the sub-basin pool with functional traits combinations falling into the observed multivariate range (i.e., convex hull; Cornwell et al. 2016) of species traits observed at a given local community. Following this logic, each community has a specific local species pool composition that was already restricted by dispersal (species pool of each sub-basin) and abiotic filters.

The null models were run 999 times for each test. We recalculated the expected functional dispersion (FDis) and the expected functional distinctiveness (FDi) in each iteration. Finally, we computed a standardized effect size (SES) as:

$$SES = \frac{observed - \mu_{null}}{\sigma_{null}}$$

where *observed* is the observed values of FDis and FDi, and  $\mu_{null}$  and  $\sigma_{null}$  are respectively the mean and the standard deviation of the expected values of FDis and FDi from the null iterations. When testing for the trait underdispersion (i.e., null model considering sub-basin species pool), negative SES values indicate that FDis or FDi was lower than expected under the null assembly. Therefore, local assemblages are assumed to have trait underdispersion patterns. Positive SES values indicate that local assemblages do not present trait underdispersion but do not necessarily have trait overdispersion patterns (Götzenberger et al. 2016). Assemblages with trait overdispersion patterns were assumed only when SES values for FDis and FDi were greater than expected according to a local species pool null model (i.e., removing the effect of abiotic filters, showed in step 3, Figure 2).

Although community assembly studies commonly consider the SES values within a range of -1.96 and 1.96 as an indication of the statistical significance (Götzenberger et al. 2016), here we used the

deviation of the SES values from 0, either positive or negative, to test how the strength of trait patterns (i.e., under and overdispersion) changes over eco-evolutionary gradients. Therefore, this strategy makes it possible to identify in which conditions each functional pattern is more likely to be predominant (Chase and Myers 2011; Siqueira et al. 2020).

#### *Drivers of the assembly patterns*

We considered three historical drivers to investigate the effect of evolutionary dynamics of Amazon Basin on the patterns of trait dispersion within the fish assemblages: i) Distance to the river mouth (km), quantified by the hydrological distance of each stream to the Amazon River mouth – Western regions (i.e., distant to the river mouth) present more speciation rates than Eastern regions (i.e., near to the river mouth; Fontenelle et al. 2021); ii) Connection to Pebas system, classified if the stream belonged (1) or not (0) to the Pebas system at ~23 Mya (*sensu* Hoorn et al. 2010); and iii) Marine incursions, classified if the stream was submerged (1) or not (0) in marine incursion at ~5 Mya, using an Elevation Models (DEM) with 30 m resolution. We chose these drivers because they have been strongly related to taxonomic and phylogenetic diversity in Amazon freshwater fish (Oberdorff et al. 2019; Salgueiro et al. 2022), due to their relationship with evolutionary processes of speciation, extinction, and dispersal.

We used two variables to summarize ecological drivers: sub-basin watercolor, and local habitat uniqueness. Amazon watercolors are an essential driver of the structure of the fish assemblages (e.g., richness and biomass; Bogotá-Gregory et al. 2020). We then classified the basin in which each stream is present in black-, clear-, and white-waters. To quantify the habitat uniqueness, we ran a multivariate homogeneity of group dispersion (PERMDISPER) with local environmental conditions of the streams (see *Data sampling* section for details), using Euclidean distances to quantify the habitat uniqueness. We then calculated the distance of each stream to the multivariate centroid of all streams. We interpreted these distances as an indication of how unique the local habitat conditions of a given stream are compared to the others. In our dataset, a typical stream can be characterized as having a substrate composed of clay, small dimensions (e.g., low depth and narrow width), and a high proportion of roots. In opposition, high values of current velocity, depth and width are conditions found in streams far from the centroid; therefore, these streams were considered as having a high habitat uniqueness (Figure S1.1).

#### *Statistical analysis*

To assess whether Amazonian stream fish assemblages present an overall tendency to trait underdispersion or trait overdispersion regardless of any predictors (historical or ecological), we used a Wilcoxon rank-sum test and compared the SES values to zero. If SES values were significantly different from zero, we investigated which ecomorphological traits are the most important to explain the functional pattern. To do that, we calculated the community-weighted trait means (CWM) for each functional dimension (i.e., PCoA axes) and related them with SES values, using Pearson correlation.

Then, to deeper understand the spatial configuration of assembly patterns, we assessed the strength of historical and ecological drivers on the SES values of FDis and  $FD_i$  with a mixed linear model (LMM), using basin identity as a random effect. The significance of each predictor variable was

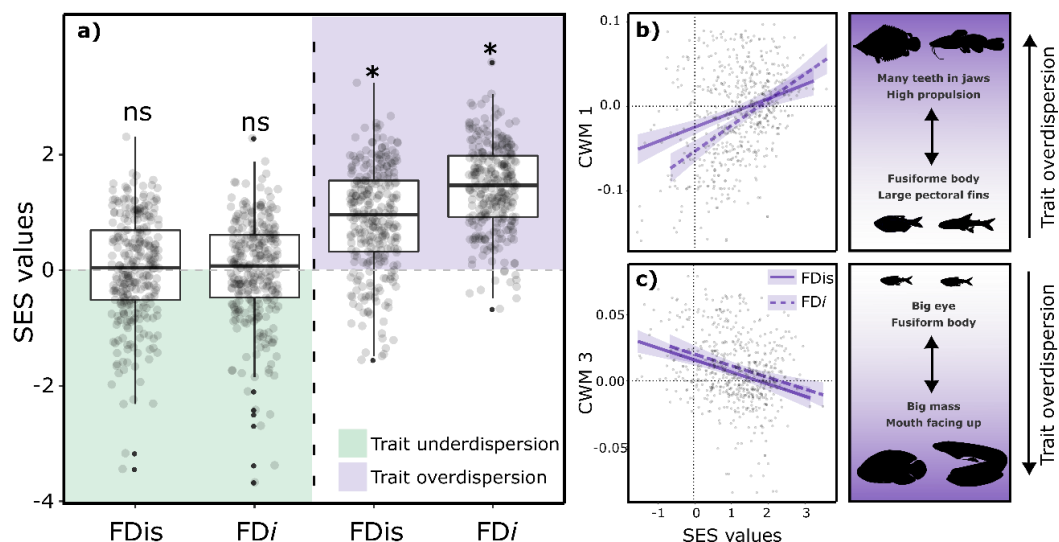
examined with Likelihood Ratio Tests (LRT). We checked the normality and heteroscedasticity by visual inspection of residual histograms of the linear models. The Variation Inflation Factor (VIF) was calculated for each predictor after model fitting, and we found that multicollinearity was not an issue in our models ( $VIF < 3$ ). We used plots of model average coefficients ( $\pm SE$ ) to represent the importance of historical and ecological predictors for the assembly patterns.

All analyses were carried out in the software R (R Foundation for Statistical Computing, Vienna, Austria) (R Core Team, 2020). Functional structure measures were calculated with Villéger' function (*multidimFD* and *quality\_funct\_space*; <http://villegier.sebastien.free.fr/Rscripts.html>), whereas linear mixed model analysis was carried out using the function *lmer* of the package *lme4* (Bates et al. 2014). The calculation of environmental uniqueness was performed with the function *betadisper*, whereas the Beals index was calculated with the function *beals*, using the package *vegan* (Oksanen et al. 2013).

## Results

### Overall patterns of the Amazonian stream fish assembly

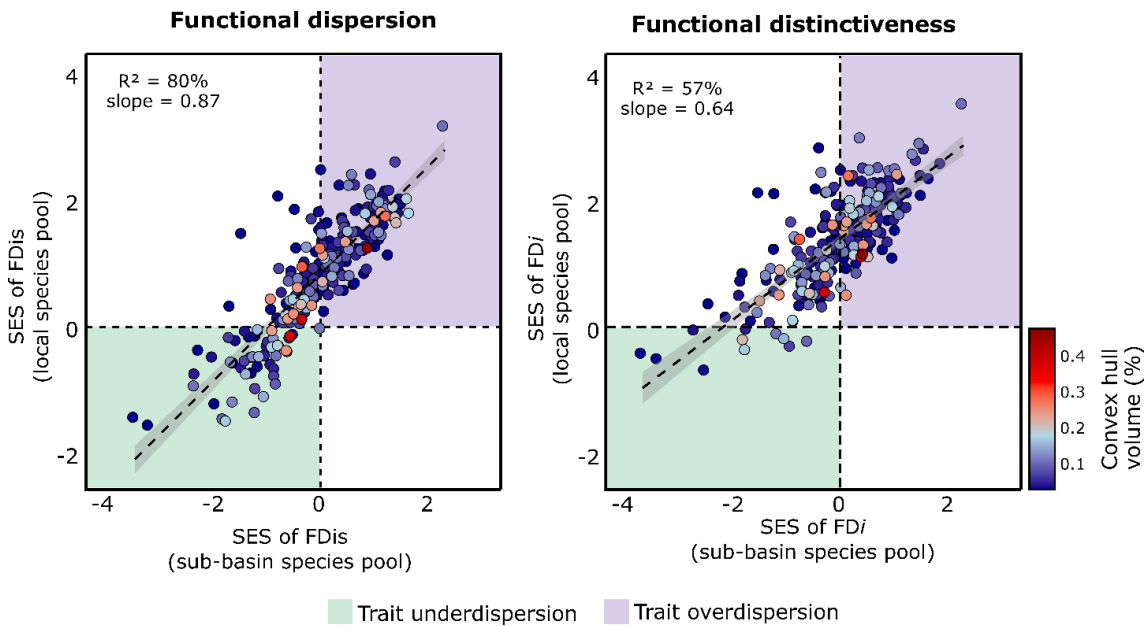
When using the sub-basin species pool, we found no evidence for an overall pattern of trait underdispersion in Amazonian stream fish assemblages for the functional dispersion (FD<sub>is</sub>;  $W = 22.1$ ;  $p = 0.82$ ) and the functional distinctiveness (FD<sub>i</sub>;  $W = 22.2$ ;  $p = 0.85$ ). However, when considering the local species pool, we observed greater trait overdispersion than expected under null assembly for both indices (FD<sub>is</sub>:  $W = 37.5$ ,  $p < 0.001$ ; FD<sub>i</sub>:  $W = 41.1$ ,  $p < 0.001$ ; Figure 3a). Fish assemblages with the highest trait overdispersion are composed of species with high number of teeth and fins surface ratio (high values for PCoA1; Table S2.3) and species with large body and terminal to superior mouth (high values for PCoA3; Table S2.3) (Figure 3b, c).



**Figure 3** Overall standard effect size (SES values) of functional dispersion (FD<sub>is</sub>) and functional distinctiveness (FD<sub>i</sub>) based on two null models that specifically test for trait underdispersion (green) and trait overdispersion (purple) patterns in 277 stream fish assemblages in Brazilian Amazonia (see Figure 2 for more details) (a). “\*” and “ns” above boxplots indicate, respectively, significant, and non-significant differences from zero. Linear regressions (b, c) show the significant relation between community

weighted trait means (CWM1 and CWM3) and SES values of FDis and FDi, with the right panels indicating the main fish morphotypes associated with the trait overdispersion pattern in assemblages (see Table S2.3).

We observed a strong positive relation between SES values computed based on the sub-basin scale versus local species pool for both FDis and FDi (Figure 4). More importantly, these patterns were not related to convex hull when considering sub-basin species pool (FDis:  $r = 0.01$ ,  $p = 0.82$ ; FDi:  $r = -0.07$ ,  $p = 0.22$ ) and local species pool (FDis:  $r = -0.01$ ,  $p = 0.92$ ; FDi:  $r = -0.07$ ,  $p = 0.24$ ). Similar pattern was observed between the relationships of the SES values and local species richness (Figure S3.1).



**Figure 4** Correlation of standard effect size (SES values) computed with the sub-basin species pool versus local species pool for the functional dispersion (FDis) and distinctiveness (FDi) of Amazonian stream fish assemblages. Green and purple areas indicate the species assemblages with narrower (trait underdispersion) and broader (trait overdispersion) trait diversity than expected under the null models using sub-basin species pool and local species pool, respectively. Color gradient (blue to red) indicates the convex hull of the streams.

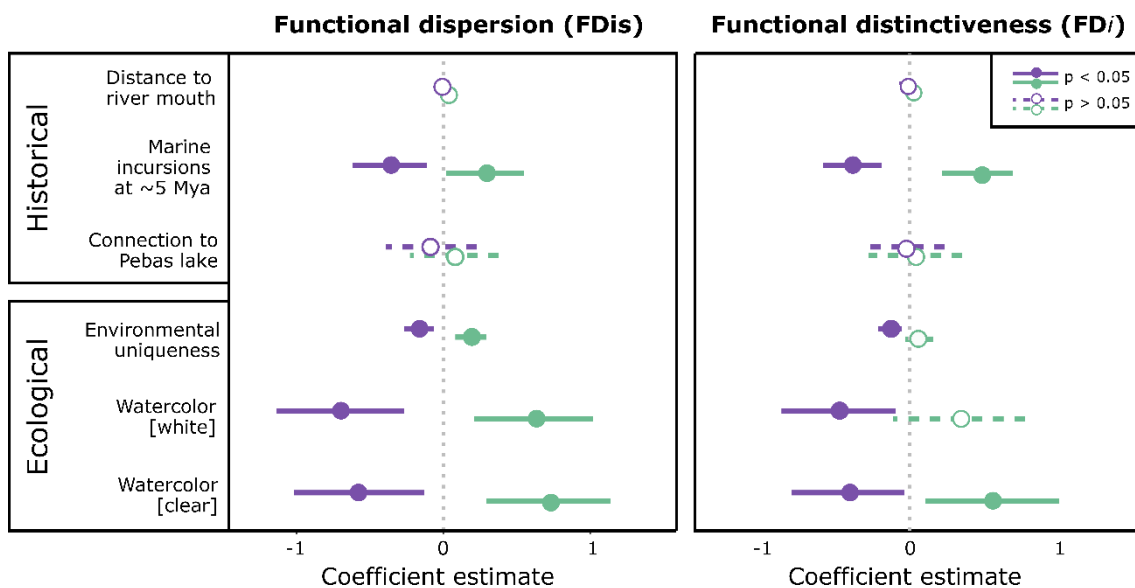
#### *Historical and ecological drivers of the functional patterns across the Amazon Basin*

The SES values of stream fish assemblages for functional dispersion (FDis) and functional distinctiveness (FDi) were related to historical and ecological drivers (Table 2). However, of the three historical drivers, only marine incursions at ~5 Mya were important to explain under and overdispersion patterns. Streams that have been submerged by seawater have fish assemblages with a trait underdispersion pattern, while elevated streams have assemblages with trait overdispersion (Figure 5). Regarding the ecological drivers, trait underdispersion was observed in fish assemblages with unique environmental characteristics (i.e., high current velocity and larger streams) and located in sub-basins with clear and white watercolors (Figure 5). On the other hand, trait overdispersion were more commonly

found in fish assemblages of streams with low current velocity and substrate composed by litter and located in black water sub-basins (Figure 5).

**Table 2** Estimates and 95% confidence interval from multiple linear mixed models (LMM) for functional dispersion (FDis) and functional distinctiveness (FDi) of Amazonian stream fish assemblage. The marginal  $R^2$  (historical and ecological drivers only) and conditional  $R^2$  (historical, ecological drivers, and sub-basin identity) values of the models are also shown. The sub-basin identity was included as a random effect on the intercept. Significant relationships are in bold.

Drivers	Sub-basin level (Trait underdispersion)		Assemblage level (Trait overdispersion)	
	FDis	FDi	FDis	FDi
<b>Historical</b>				
Distance to Amazon River mouth	0.02 (-0.03 to 0.08)	0.01 (-0.04 to 0.07)	-0.02 (-0.08 to 0.03)	-0.02 (-0.07 to 0.02)
Marine Incursions	<b>0.33 (0.01 to 0.55)</b>	<b>0.47 (0.21 to 0.70)</b>	<b>-0.39 (-0.61 to -0.11)</b>	<b>-0.40 (-0.58 to -0.18)</b>
Pebas connection	0.06 (-0.27 to 0.37)	0.02 (-0.27 to 0.35)	-0.07 (-0.39 to 0.22)	-0.02 (-0.29 to 0.23)
<b>Ecological</b>				
Color [White]	<b>0.58 (0.17 to 0.97)</b>	0.36 (-0.08 to 0.81)	<b>-0.69 (-1.13 to -0.26)</b>	<b>-0.46 (-0.85 to -0.07)</b>
Color [Clear]	<b>0.71 (0.29 to 1.14)</b>	<b>0.55 (0.11 to 1.01)</b>	<b>-0.56 (-1.01 to -0.12)</b>	<b>-0.40 (-0.80 to -0.03)</b>
Environmental uniqueness	<b>0.10 (0.01 to 0.22)</b>	0.05 (-0.02 to 0.15)	<b>-0.15 (-0.26 to -0.06)</b>	<b>-0.10 (-0.18 to -0.02)</b>
Models $R^2$ (marginal/conditional)	0.07/0.12	0.06/0.14	0.11/0.18	0.10/0.19



**Figure 5** Influence of historical and ecological drivers on standard effect size (SES) values of functional dispersion (FDis) and functional distinctiveness (FDi) for null models that test for trait underdispersion (green) and overdispersion (purple) in 288 stream fish assemblages of Brazilian Amazonia.

## Discussion

There is still an open debate on how tropical communities are structured and the relative importance of historical or ecological drivers in the assembly process (Peres-Neto 2004; Kraft and Ackerly 2010; Jarzyna et al. 2021). Over the biogeographical range of Amazon fish, the stream fishes have striking morphological and trophic differences that allow them to explore heterogeneous habitats



and resources (Figure S2.3). In accordance, the functional diversity of local assemblages was greater than could be expected by chance, expressed by a pattern of trait overdispersion. Therefore, fish assemblages comprised species with more dissimilar trait combinations than expected, particularly those related to locomotion and trophic ecology. The presumed hydrological stability of Amazonian streams appears as a possible mechanism favoring the assemblages composed of species with complementary traits (Figure 3). Moreover, we showed that this pattern was independent of the local number of species, suggesting that the taxonomic richness does not necessarily translate into the community assembly patterns in Amazonian stream fishes. Our results also highlighted the interplay between historical and ecological drivers in modulating the trait diversity of assemblages. This ultimately reinforces the perception that, although thought to be mostly structured by local factors (Warren et al. 2014), the traits diversity of local communities is also defined by processes acting at large spatial and temporal scales (Tóth et al. 2019).

#### *Overall assembly pattern of the Amazonia stream fishes*

We found an overall tendency for fish assemblages being composed of species more functionally different from each other than expected by chance (i.e., trait overdispersion; Figure 3a). This finding is not in accordance with those studies in streams with strong influence of flow variation during rain (Rodrigues-Filho et al. 2017; Bower and Winemiller 2019b). The hydrological disturbances act as an environmental filter selecting species with suitable traits to overcome the limitations imposed by drag (e.g., depressed bodies and small size) or able to recolonize the sites after severe hydrological events. Conversely, Amazonian pristine streams are presumed to have relative hydrologic stability (Espírito-Santo et al. 2009) and oligotrophic waters (Mendonça et al. 2005). Even when the rain is heavy, the ichthyofauna of small streams is buffered against disassembling due to lateral connections with temporary pools, acting as a refuge for several species (Espírito-Santo and Zuanon 2017). Therefore, when considering the entire flood zone (streams plus pools), fluctuations in fish species composition and abundance were smoothed over the hydrological cycle. Thus, Amazonian streams are presumed to be composed of stable fish populations that probably compete for limited resources (i.e., habitat and food) throughout the year and span a huge variety of morphological and trophic traits (Figure S2.2). Such as the petite *Microcharacidium eleotrioides* (maximum body length = 21 mm) and the big, marbled swamp eel *Synbranchus marmoratus* (maximum body length > 150 cm) that use lateral pools to forage, posteriorly recolonizing the adjacent stream (Espírito-Santo et al. 2013; Espírito-Santo and Zuanon 2017). Consequently, the ratio of resource demand/supply in Amazonian streams should be high enough to cause competitive exclusion between fish species sharing similar ecological requirements, and therefore creating an overall pattern of trait overdispersion within species assemblages (Mouillot et al. 2007; Montaña et al. 2014).

We also found support for the paradigm that feeding, and locomotion traits should be used to detect the importance of biotic interactions (Jackson et al. 2001; Montaña and Winemiller 2009). For instance, fish assemblages composed of large body species with many teeth in jaws, high fins surface ratio and terminal to superior mouth tend to present species with complementary traits (trait overdispersion; Figure 3b, c). This indicates that species have morphological and trophic characteristics that allow them to explore the same microhabitat but in different fashion. A fascinate example of fine

resource partition is documented for species that resemble dead leaves for hunting and avoid predators. The dead leaf disguise for hunting is documented for the leaf-fish *Monocirrhus polyacanthus* that mimics dead leaves and moves unobtrusively towards the intended prey using its invisible fins for capturing small characins (Catarino and Zuanon 2010). On the other hand, the crypt catfish *Helogenes marmoratus* lie on its side within aquatic leaf litter for defense against predators, a strategy that is enhanced by the laterally compressed body and the long anal fin (Sazima et al. 2006). A lesser tendency for trait overdispersion was observed in assemblages with a higher predominance of fusiform body fishes with big eyes. These species are characterized by their opportunistic feeding strategies, allowing them to live together regardless of sharing similar morphological traits (Brejão et al. 2013). For example, the characins *Bryconops giacopinii* and *Iguanodectes geisleri*, although having similar morphotypes (i.e., small-body, big eye and body shape surface), can change their diet when in syntopy (Barros et al. 2017). Morphological resemblance can also be observed in Amazonian streams, where the small-body characin *Gnathocharax steindachnerina* joins schools of the small mouthed-butterfly fish *Carnegiella strigata* to catch water strider bugs at the water surface (i.e., insectivorous; Carvalho et al. 2007). Indeed, Amazonian streams can support many species of characins with similar morphological and trophic traits, which can explain the global invariant relationship between species richness and trait overdispersion pattern (Figure S3.1).

#### *Historical drivers of assembly patterns*

The Amazon Basin has suffered with marine incursions ~5 Mya ago when sea rise from 50 to 100 m for a duration of ~800 thousand years (Haq et al. 1987; Hoorn et al. 2010). These events could have eliminated lowland freshwater habitats and led to the high extinction of aquatic biota. Thus, marine fluctuation can be considered a strong biogeographical filter that may promote past extinctions in portions of lowland Amazonia Basin, while elevated areas have experienced relative stability and low extinction rates. Our results are in line with this expectation since that species assemblage submerged by seawater presents smaller trait diversity (i.e., trait underdispersion) than elevated assemblages not affected by marine incursions (Figure S4.1). By inspecting the relation between SES values obtained from the null model considering the sub-basin species pool and CWM1 and CWM3 (Table S2.4), we observed that assemblages that have been submerged by sea at ~5 Mya present a predominance of species with functional traits strongly related to dispersal ability, such as body transversal surface and caudal peduncle-throttling (Gatz 1979; Griffiths 2006). Similar patterns are observed in studies carried out in previously glaciated assemblages, where Northern assemblages are dominated by fish with high dispersal ability (Blanchet et al. 2010; Su et al. 2022). Nevertheless, this pattern is not exclusive to freshwater fish (Dobrovolski et al. 2012), suggesting that past extinctions can indeed represent an important historical filter selecting those species with high dispersal ability. Conversely, Amazonian species assemblages that have been not submerged by sea at ~5 Mya are composed of functionally complementary species (i.e., trait overdispersion) when compared to assemblages that have been submerged. This is exemplified by the influence of historical disturbance in Neotropical stream fish assemblages (Rodrigues-Filho et al. 2018). Low rates of historical extinctions enhance the regional functional diversification, enabling species to finely partition resources across space (i.e., trait overdispersion). Indeed, the strong relationship between SES values obtained from the null model considering the local species pool and the CWM1 and

CWM3 (Table S2.3), suggests that streams that have been not submerged by sea are composed of species with distinct feeding strategies. This is the case for the traits oral-gape and pectoral fin position, which are strongly influential on CWM3. Species with extreme values for these traits (e.g., grazers of the Loricariidae family) have a modified ventral-suckermouth adapted to graze on algae and biofilms (Pagotto et al. 2011). In addition, big species with many teeth in jaws (CWM1) feed on other animals, including fishes, which minimize the overlap with the grazers, allowing thereby the local coexistence of species functionally complementary.

Although the regional taxonomic and phylogenetic diversity of freshwater ichthyofauna throughout Amazonia Basins are strongly related to the speciation gradient (Oberdorff et al. 2019; Salgueiro et al. 2022), our results show no significant effect of the distance to River mouth and Pebas connection on assembly patterns. Although empirical support for the importance of speciation on local assembly is mixed (Vellend, 2016), weaker importance can be observed under strong niche conservatism (Harrison and Grace 2007). In this case, two regions could have striking differences in the richness of species pool but only slight differences in traits diversity (i.e., sister species have similar traits; Price 2010). This seems like be the case for fish species that inhabit small streams, which present high morphological and trophic ecology convergence; different lineages could similarly explore local habitats (Montaña and Winemiller 2013; Bower et al. 2021).

#### *Ecological drivers of assembly patterns*

Fish composition is largely influenced by the watercolor of Amazonia rivers (Bogotá-Gregory et al. 2020). Due to their physical and chemical characteristics, watercolor can act as a dispersal filter, influencing the outcome of biotic interactions (Etienne and Olff 2005). Amazon white water is nutrient-rich and have neutral pH (pH ~ 7) and harbors higher regional richness and abundance of ichthyofauna than clear and black waters (Bogotá-Gregory et al. 2020). Highly productive environments provide more opportunity for more species with different traits to coexist (Chesson 2000). This is the case for white water that have more availability of aquatic resources (e.g., nutrients, zooplankton, and aquatic insect larvae) than black and clear (Fernandes et al. 2004). Because of that, we expected to find higher importance of trait overdispersion in fish assemblages of streams embedded in basins with white than in basins with black and clear waters. However, we registered the opposite, wherein sub-basins with black water the local assemblages showed more overdispersion tendency than white and clear waters (Figure S4.2). This is an unexpected and interesting result because black water is stained by tannins and humic acids leached from vegetation promotes low pH (pH < 5) and scarce autochthonous productivity, conditions that impose environmental filters to fish species unfitting these conditions (Bogotá-Gregory et al. 2020). One possible explanation might derive from the high lineage's diversification of freshwater fish in Amazon black waters (Salgueiro et al. 2022). For instance, the Negro River is the third largest in the world and their physical and chemistry conditions offers a unique condition for species adaptation (Goulding et al. 1989), such as the small subterranean catfish *Preatobius* sp. has small eyes and lack of melanin pigment in the skin.

Our results also depict an effect of instream abiotic conditions on community assembly patterns. We registered that a unique combination of instream environmental conditions (e.g., high current velocity

and channel dimensions) enhances the importance of trait underdispersion (Figure S4.3). Water current imposes a strong drag limitation for stream fishes, favoring those species capable of maintaining the position in the water column even when the velocity is high (Gatz 1979). Species with morphotypes not adapted to live in faster habitats pay an enormous energetic cost to perform essential functions such as locomotion and foraging. Thus, streams with unique conditions limit the species colonization and create a trait underdispersion pattern, because only those species with traits suited for overcoming water drag forces can establish and persist (Bower and Winemiller 2019b). In opposition, a condition of low current velocity relaxes the limitation on morphology imposed by drag favoring the coexistence of species with a high diversity of traits (e.g., trait overdispersion) (Kovalenko et al. 2012). Together, these results are in line with the traditional idea that stressful environments exclude species with unsuitable traits, resulting in species assemblages with narrower trait diversity (i.e., trait underdispersion) (Weiher and Keddy 1995; Chauvet et al. 2017).

## Conclusions

This study gives insights into the assembly of Amazonian stream ichthyofauna, showing that coexisting species tend to be functionally more different than expected under null expectations. This result contrasts with the findings that traditionally indicate a stronger effect of environmental filtering in stream fish assemblages. This could be partly explained by the presumed hydrological stability of Amazonia streams. In addition, we found that past extinction events, particularly the marine incursions, can influence the contemporary patterns of Amazonia stream fishes, reinforcing the need to consider the historical legacy to understand the contemporary faunas. This outcome suggests that historical and ecological drivers influence assembly in a simultaneous manner. Thus, this study demonstrates the importance of understanding processes acting in different temporal scales (i.e., evolutionary, and contemporary) in relation to community assembly of the Amazonia fish assemblages, one of the highest diverse on Earth.

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**Author contribution statements:** CASRF, FBB and RPL originally formulated the idea; CASRF, JZ and RPL conducted fieldwork; CASRF, GNS and RPL analyzed the data; CASRF lead the writing process; FBB, JZ, GNS, and RPL actively contributed to discuss the results and write the manuscript. All authors read and approved the final manuscript.

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## OECOLOGIA

## SUPPORTING INFORMATION

Historical and ecological drivers of community assembly of the Amazonia stream fish assemblages

**Carlos Alberto Sousa Rodrigues-Filho, Fabricio Beggiato Baccaro, Jansen Zuanon, Gilberto**

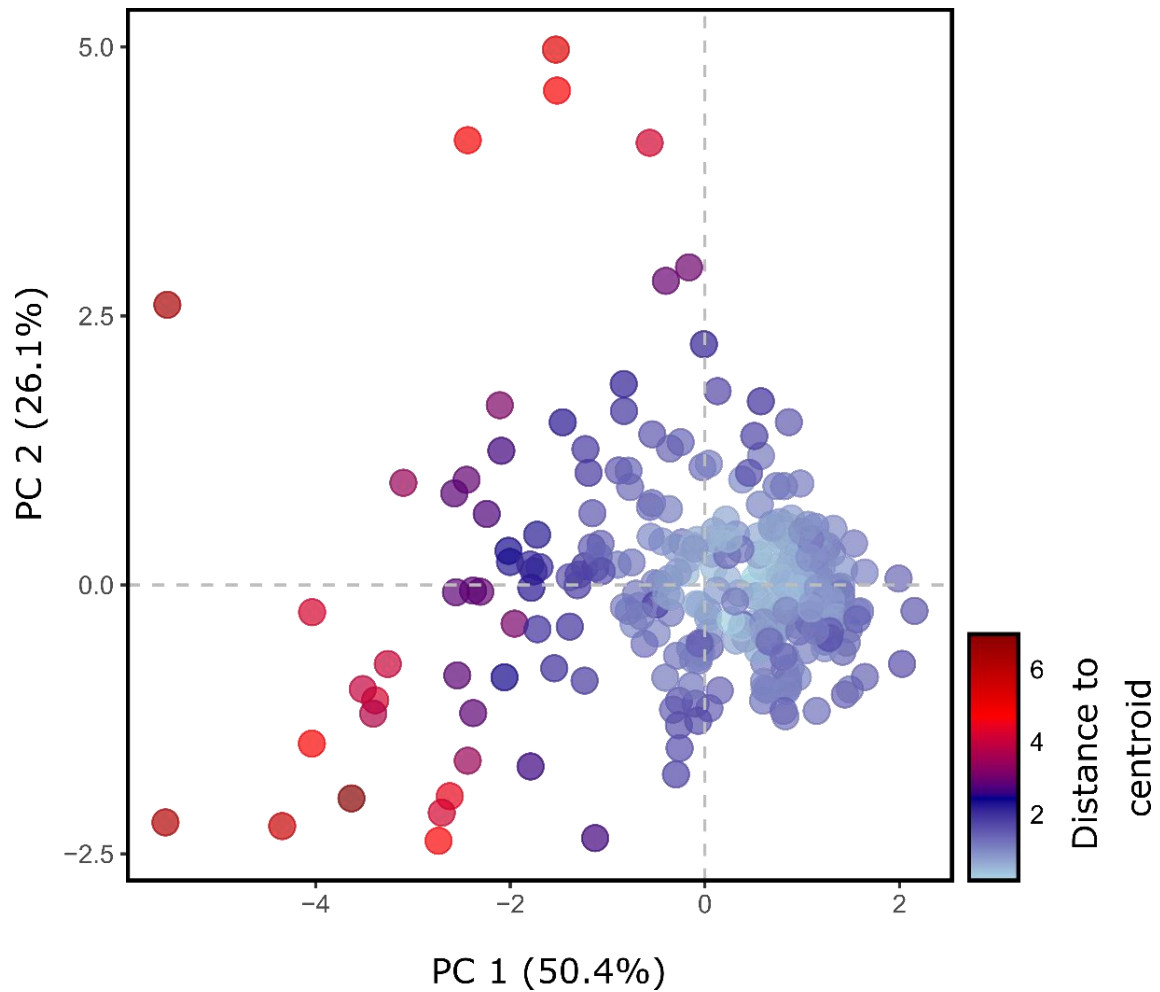
**Nepomuceno Salvador, Rafael Pereira Leitão**

**Supporting information 1: Local habitat conditions**

We used a standardized protocol to characterize local habitat and sampling stream fish assemblages from Amazonia. We first blocked with nets (3 mm mesh) the extremities of each sampling site delimiting a 50-m stretch and measured physical and chemical variables. Later, three collectors actively sampled for fish with seines and hand nets during two hours in an upstream direction. The collected fishes were euthanized with a lethal concentration of anesthetics (Eugenol), fixed in 10% formalin, and later stored in ethanol 70%. Collecting and euthanizing fishes were conducted under permits from SISBio/ICMBio and institutional committees for ethics in research with animals in Brazil. Voucher specimens were deposited in the fish collections of the Instituto Nacional de Pesquisas da Amazônia (Manaus, Amazonas State, Brazil).

**Table S1.1** Habitat conditions measured in each of the 305 streams sampled for Brazilian Amazonia stream fish.

Group	Variable	Unit	Mean	Min	Max
Channel Structure	Mean water velocity	cm s <sup>-1</sup>	0.20	0.00	1.00
	Mean depth	m	0.20	0.01	0.94
	Mean width	m	2.43	0.44	15.22
Substrate	Sand	%	0.23	0.00	0.88
	Clay	%	0.07	0.00	0.91
	Litter	%	0.46	0.00	0.97
	Trunk	%	0.05	0.00	0.38
	Macrophyte	%	0.01	0.00	0.36
	Root	%	0.10	0.00	0.55
	Pebble	%	0.05	0.00	0.88



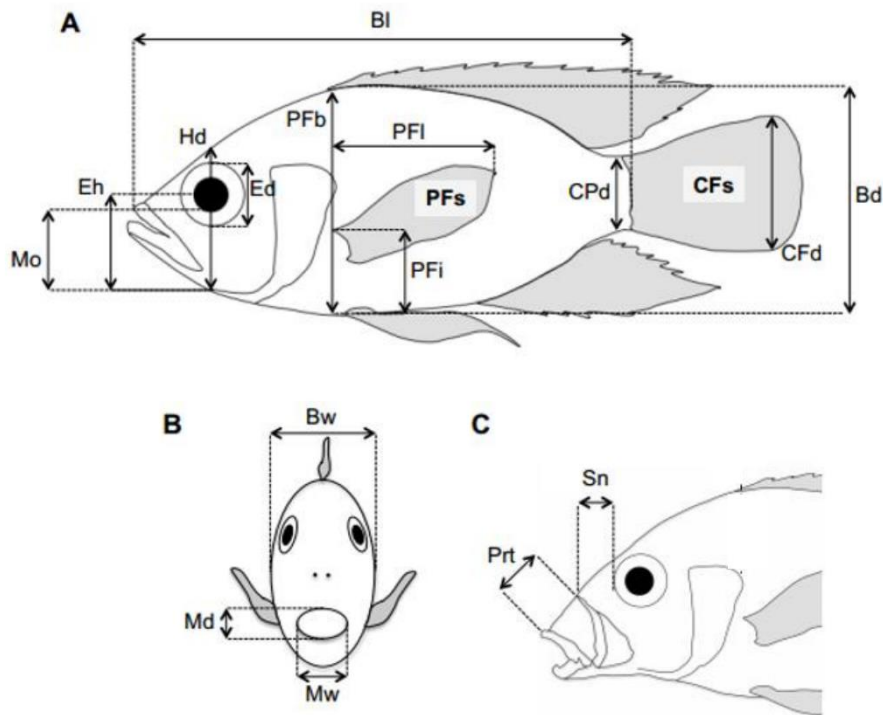
**Figure S1.1** Principal component analysis (PCA) based on local habitat metrics to visualize the environmental uniqueness of 288 Brazilian Amazon streams. Color gradient represents the Euclidean distance of each stream to the centroid (i.e., environmental uniqueness). Loadings of abiotic variables are provided in Table S1.2.

**Table S1.2** Loadings of instream variables of the Principal Components Analysis (PCA), conducted to quantify the streams' environmental uniqueness.

Group	Variable	PC 1 (50.4 %)	PC 2 (26.1 %)
Channel	Velocity	-0.55	0.82
	Width	-0.80	-0.37
	Depth	-0.84	-0.20
Substrate	Sand	-0.16	0.27
	Clay	-0.15	0.04
	Litter	0.34	-0.32
	Trunk	-0.20	-0.06
	Macrophyte	-0.19	0.03
	Root	-0.08	0.04
	Pebble	-0.08	0.14

## Supporting information 2: Functional trait assessment

From the ecomorphological analysis (17 measures; Figure S2.1) and body mass (taken from a digital balance with an accuracy of 0.001g), we obtained 15 functional traits (Table S2.1) related to locomotion capacity, food acquisition and water column occupation for 183 fish species (according to Leitão et al., 2016). These measures were taken from 3-10 individuals per species. We used the mean values of each trait measured (see Table S2.1) among individuals of each species.



**Figure S2.1** Seventeen morphological traits measured for fish on digital pictures (A): *Bd* body depth, *CPd* caudal-peduncle minimal depth, *CFd* caudal-fin maximum depth, *CFs* caudal-fin surface, *CPd* caudal fin-depth, *PFi* distance between the insertion of pectoral fin to the bottom of the body, *Pfb* body depth at the level of the pectoral-fin insertion, *PFl* pectoral-fin length, *PFs* pectoral-fin surface, *Hd* head depth along the vertical axis of the eye, *Ed* eye diameter, *Eh* distance between the center of the eye to the bottom of the head, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis; and with digital caliper (B, C): *Bw* body width, *Md* mouth depth, *Mw* mouth width, *Sn* snout length, *Prt* protrusion length.

**Table S2.1** List of 15 functional traits measured from the ecomorphological measurements of the fish species, with their ecological meanings. Adapted from Leitão et al. (2016).

Functional traits	Calculation/Class	Abbreviation	Nature	Ecological meaning	References
Teeth shape	Absent Canine Comb-shaped Conic Incisiform Molariform Aliasing multicuspid Spoon-shaped Tricuspid Villiform	Tsh	Nominal	Nature of food items captured and feeding method	Adapted from Gatz (1979)
Number of teeth	Mean number of teeth between upper and lower jaws	Tnu	Continuous	Nature of food items captured and feeding method	Adapted from Gatz (1979)
Gill-raker shape	Absent Short/ sparse Intermediate Long/ numerous	Rsh	Ordinal	Filtering ability and gill protection	Adapted from Sibbing & Nagelkerke (2001)
Mouth-protrusion length	$\frac{Prt}{Sn}$	Prt	Continuous	Feeding method	Adapted from Gatz (1979)
Oral-gape surface	$\frac{Mw * Md}{Bw * Bd}$	Osf	Continuous	Size of food items captured	Adapted from Karpouzi & Stergiou (2003)
Oral-gape shape	$\frac{Md}{Mw}$	Osh	Continuous	Method to capture food items	Karpouzi & Stergiou (2003)
Oral-gape position	$\frac{Mo}{Hd}$	Ops	Continuous	Feeding method in the water column	Adapted from Sibbing & Nagelkerke (2001)
Eye size	$\frac{Ed}{Hd}$	Edst	Continuous	Prey detection	Adapted from Boyle & Horn (2006)

Eye position	$\frac{Eh}{Hd}$	Eps	Continuous	Vertical position in the water column	Gatz (1979)
Body transversal shape	$\frac{Bd}{Bw}$	Bsh	Continuous	Vertical position in the water column and hydrodynamism	Sibbing & Nagelkerke (2001)
Body transversal surface	$\frac{\ln[\frac{\pi}{4} * Bw * Bd] + 1}{\ln(Mass + 1)}$	Bsf	Continuous	Mass distribution along the body for hydrodynamism	Villéger <i>et al.</i> , 2010
Pectoral-fin position	$\frac{Pfi}{PFb}$	PFps	Continuous	Pectoral fin use for maneuverability	Dumay <i>et al.</i> , (2004)
Aspect ratio of the pectoral fin	$\frac{PFl^2}{PFs}$	FPar	Continuous	Pectoral fin use for propulsion	Adapted from Fulton <i>et al.</i> , (2001)
Caudal-peduncle throttling	$\frac{CFd}{CPd}$	Cpt	Continuous	Caudal propulsion efficiency through reduction of drag	Webb (1984)
Aspect ratio of the caudal fin	$\frac{CFd^2}{CFs}$	CFar	Continuous	Caudal fin use for propulsion and/or direction	Webb (1984)
Fins surface ratio	$\frac{2 * PFs}{CFs}$	Frt	Continuous	Main type of propulsion between caudal and pectoral fins	Villéger <i>et al.</i> , 2010
Fins surface to body size ratio	$\frac{(2 * PFs) + CFs}{\frac{\pi}{4} * Bw * Bd}$	Fsf	Continuous	Acceleration and/or maneuverability efficiency	Villéger <i>et al.</i> , 2010
Body mass	$\log(Massa + 1)$	LogM	Continuous	Metabolism, endurance, and swimming ability	Villéger <i>et al.</i> , 2010



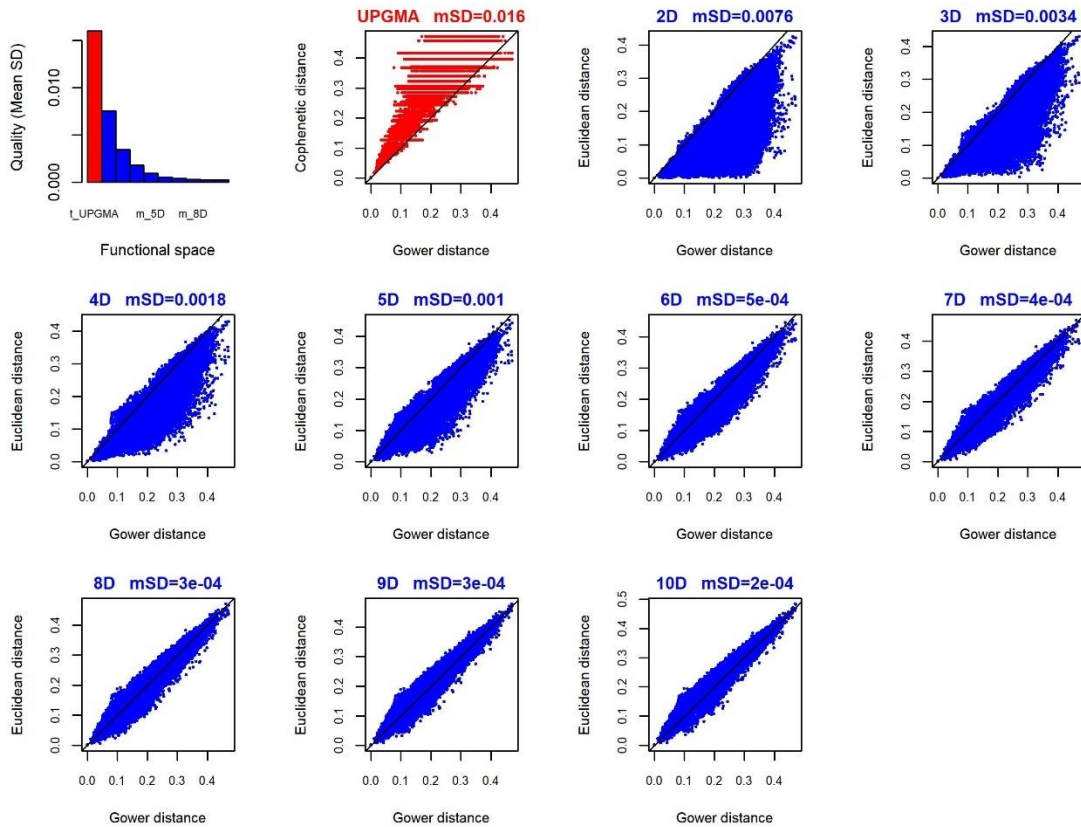
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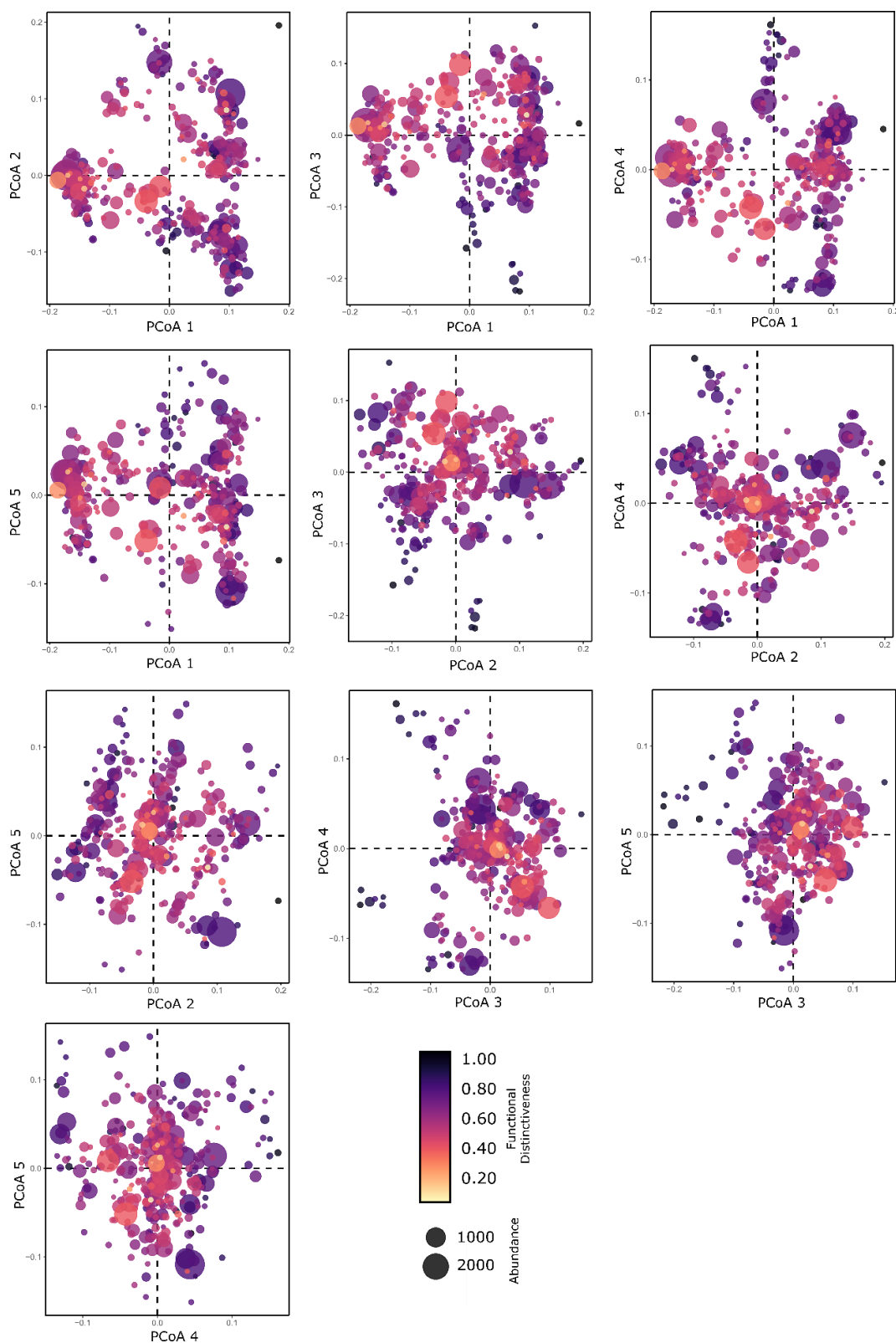
**Table S2.2** Functional trait loadings explained variance and biological interpretation of each Principal Component axes (PC).

Traits	Abbreviation	PCO1	PCO2	PCO3	PCO4	PCO5
Mass	logM	0.329	-0.944	-0.988	0.152	-0.995
Oral-gape surface	Osf	-0.733	0.681	-0.625	0.781	-0.170
Oral-gape shape	Osh	-0.969	0.245	0.671	-0.741	-0.931
Oral-gape position	Ops	-0.606	0.795	-0.937	-0.349	-0.601
Mouth-protrusion length	Prt	0.319	0.948	-0.016	1.000	-0.953
Eye size	Edst	-0.568	0.823	0.964	0.267	-0.810
Eye position	Eps	0.786	-0.618	-0.620	0.785	0.695
Body transversal shape	Bsh	-0.903	0.429	-0.308	-0.951	-0.743
Body transversal surface	Bsf	0.044	0.999	0.995	-0.100	0.998
Pectoral-fin position	PFps	0.665	0.747	-0.642	0.767	0.390
Aspect ratio of the pectoral fin	PFar	-0.999	-0.035	0.932	-0.362	0.385
Caudal-peduncle throttling	CPt	-0.394	-0.919	0.741	0.672	-0.492
Aspect ratio of the caudal fin	CFar	-0.837	-0.547	0.712	0.703	-0.865
Fins surface ratio	Frt	0.975	-0.223	0.594	0.805	-0.363
Fins surface to body size ratio	Fsf	0.590	0.807	0.571	0.821	-0.254
Number of teeth	Tnu	1.000	0.025	-0.514	0.858	-0.049
Gill-raker shape	Absent	0.045	0.042	-0.086	-0.048	0.057
	Short/sparse	0.074	-0.012	0.020	-0.009	-0.014
	Intermediate	-0.111	0.009	-0.017	0.029	0.009
	Long/numerous	-0.103	0.008	0.016	-0.017	0.004
Teeth shape	Canine	-0.037	-0.032	-0.006	0.000	-0.070
	Comb-shaped	0.088	-0.093	0.076	0.036	0.008
	Conic	0.055	0.071	-0.006	-0.006	-0.004

Incisiform	-0.026	-0.057	0.007	-0.047	-0.066
Molariform	-0.128	-0.083	-0.079	-0.011	-0.073
Aliasing multicuspid	-0.065	-0.016	0.063	-0.031	-0.005
Absent	0.046	-0.071	-0.031	-0.108	0.039
Spoon-shaped	0.107	-0.135	0.062	0.037	-0.033
Tricuspid	-0.147	-0.018	0.001	-0.002	-0.006
Viliform	0.060	-0.069	-0.049	0.083	0.039



**Figure S2.2** Evaluation of the quality of the functional space. Barplot shows the mean squared deviation (mSD) between observed and reduced functional distance among species, using dendrogram (red) and functional space (blue) derived from the Principal Coordinate Analysis (PCoA). Following Maire et al. (2015) we chose the number of PCoA axes that show  $mSD < 0.002$ . Thus, we opted to retain five PCoA axes to carry out the functional analyses.



**Figure S2.3** Five-dimensional functional space of the regional pool of stream fish from the Brazilian Amazon (375 species). Each plot represents two axes of a Principal Coordinate Analysis (PC), where species are plotted with circles according to their respective trait values. The circle size represents the species regional abundance. Color gradient represents the mean functional distinctiveness ( $D_i$ ) of each species considering all streams.

**Table S2.3** Pearson correlations (r) and significance (p) between community-weighted trait mean (CWM) and SES values of functional dispersion (FDis) and functional distinctiveness (FDi) obtained from a null model considering the local species pool.

	FDis		FDi	
	r	p	r	p
<b>CWM 1</b>	<b>0.277</b>	<b>&lt;0.001</b>	<b>0.404</b>	<b>&lt;0.001</b>
CWM 2	0.064	0.277	0.081	0.170
<b>CWM 3</b>	<b>-0.300</b>	<b>&lt;0.001</b>	<b>-0.237</b>	<b>&lt;0.001</b>
CWM 4	0.065	0.268	0.099	0.091
CWM 5	0.007	0.891	-0.018	0.745

**Table S2.4** Pearson correlations (r) and significance (p) between community-weighted trait mean (CWM) and SES values of functional dispersion (FDis) and functional distinctiveness (FDi) obtained from a null model considering the sub-basin species pool.

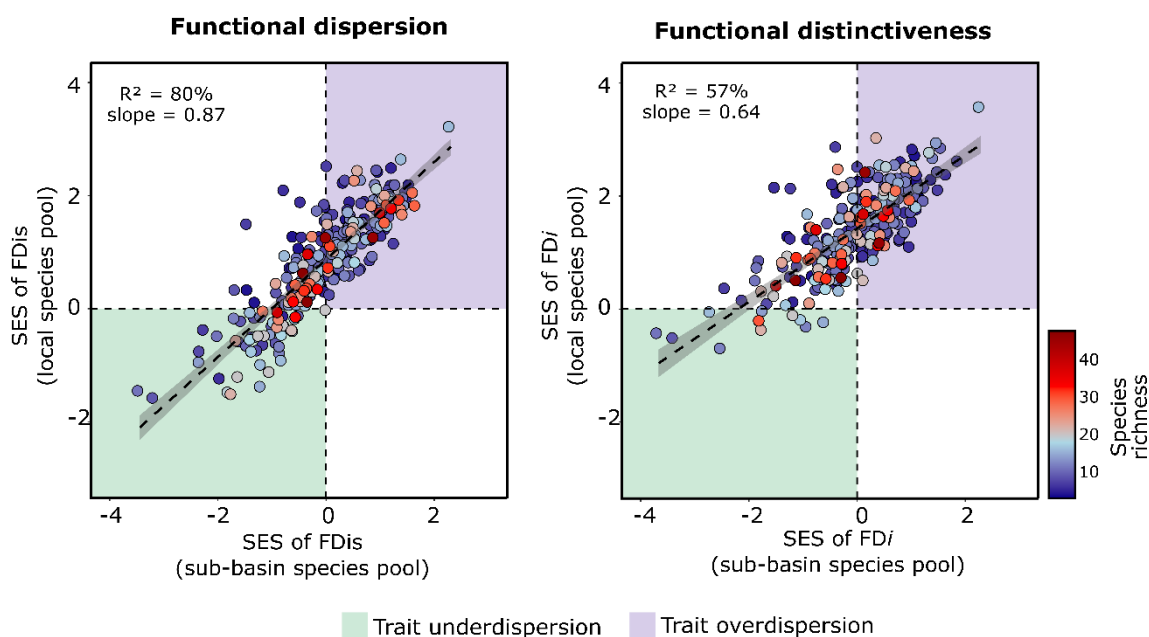
	FDis		FDi	
	r	p	r	p
<b>CWM 1</b>	<b>0.223</b>	<b>&lt;0.001</b>	<b>0.361</b>	<b>&lt;0.001</b>
CWM 2	0.036	0.534	0.067	0.254
<b>CWM 3</b>	<b>-0.249</b>	<b>&lt;0.001</b>	<b>-0.202</b>	<b>&lt;0.001</b>
CWM 4	0.084	0.153	<b>0.151</b>	<b>0.014</b>
CWM 5	0.019	0.746	0.021	0.711

### Supporting information 3: Relationships between SES values and species richness and convex hull volume

Filtering framework has been largely applied in ecological/biogeographical studies to test whether local communities display trait underdispersion or overdispersion patterns (Mouillot *et al.*, 2007; Chauvet *et al.*, 2017; Bosch *et al.*, 2021). The heart of this studies is the way of estimation of the species pool and the null model applied to create random communities (Weiher and Keddy, 1995; Weiher *et al.*, 2011). As a result, communities are inferred to have trait under or overdispersion patterns. However, because these two assembly patterns need different species pool estimation to be observed, different null models are necessary to disintegrate their isolated effects (de Bello *et al.*, 2012). To deal with this, we carried specific null models to test for trait underdispersion and for trait overdispersion patterns. Nevertheless, there are potential caveats in the decisions made during null model constructions.

Specifically, to test for trait overdispersion it is necessary control for abiotic filters that select species from a regional pool into local pool composed of those species capable to tolerate local conditions. The local species pool was estimated by using the locally present trait combinations of species. In sum, those species present in the sub-basin pool having trait combinations falling in the observed range of those species found in local assemblages were assumed to compose the local species pool (i.e., convex hull; Conwell and Ackerly, 2006). The use of the convex hull approach to estimate the local species pool would be sensible to local species richness where poor assemblages should have low convex hull volume and thereby low local species pool richness (Villéger *et al.*, 2008). Thus, greater tendency for trait overdispersion would be observed in streams with low species richness than in streams

with high species richness. However, the invariant relationship between the convex hull volume (Figure 4 in the main text) and the species richness (Figure S3.1) with SES values indicated that the criteria used to estimate the local species pool was not enough to blur the reliability of our results.



**Figure S3.1** Correlation of SES values computed with the sub-basin species pool versus local species pool for the functional dispersion (FDis) and distinctiveness (FDi) of stream fish assemblages in Amazonia. Green and purple areas indicate the species assemblages with narrower (trait underdispersion) and broader (trait overdispersion) trait diversity than expected under the null models using sub-basin species pool and local species pool, respectively. Color gradient (blue to red) indicates the species richness of the streams. We did not observe significant relationship between local species richness and the SES values derived from null models considering the sub-basin species pool (FDis:  $r = -0.17$ ,  $p = 0.86$ ; FDi:  $r = -0.2$ ,  $p = 0.08$ ) and the local species pool (FDis:  $r = -0.19$ ,  $p = 0.11$ ; FDi:  $r = -0.21$ ,  $p = 0.07$ ).

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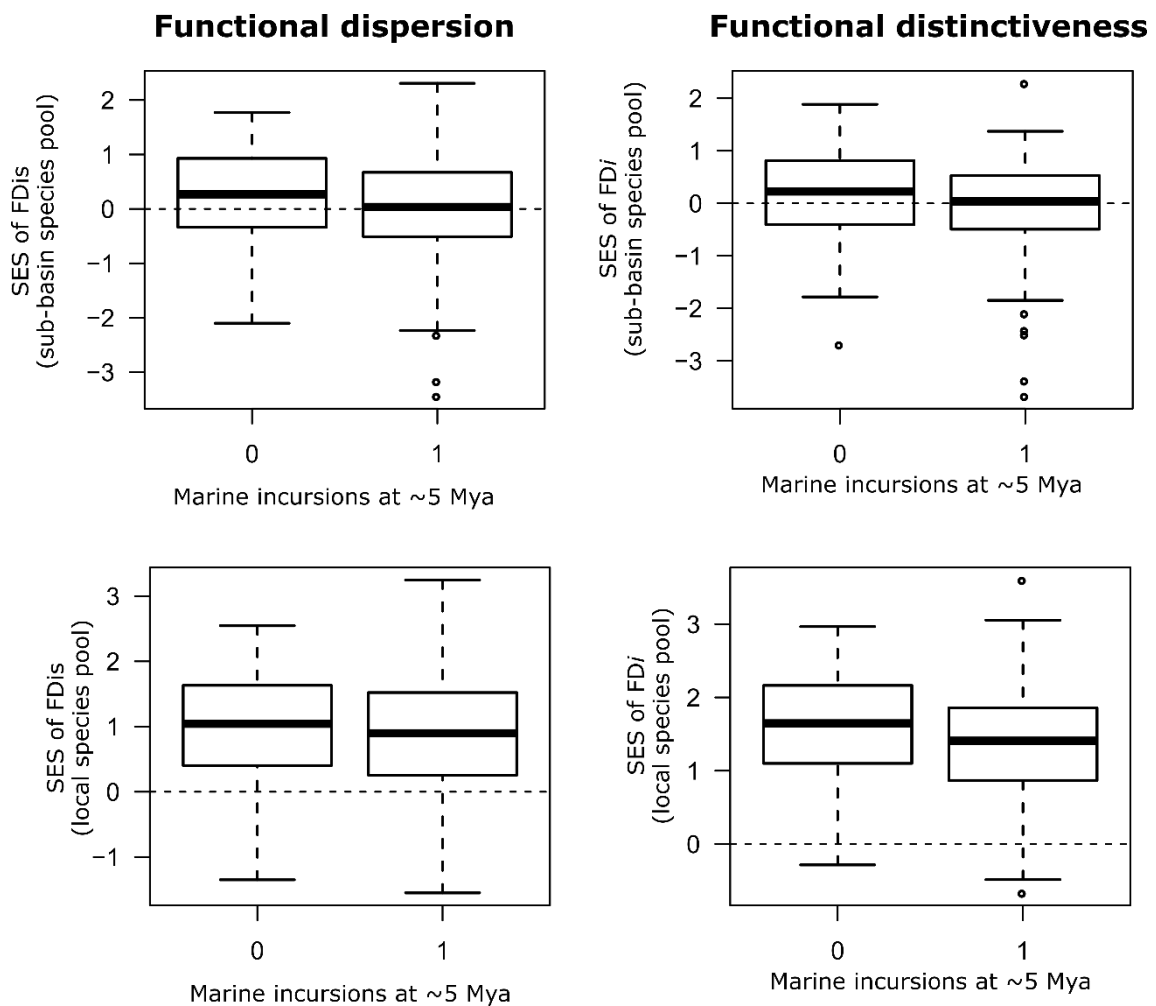
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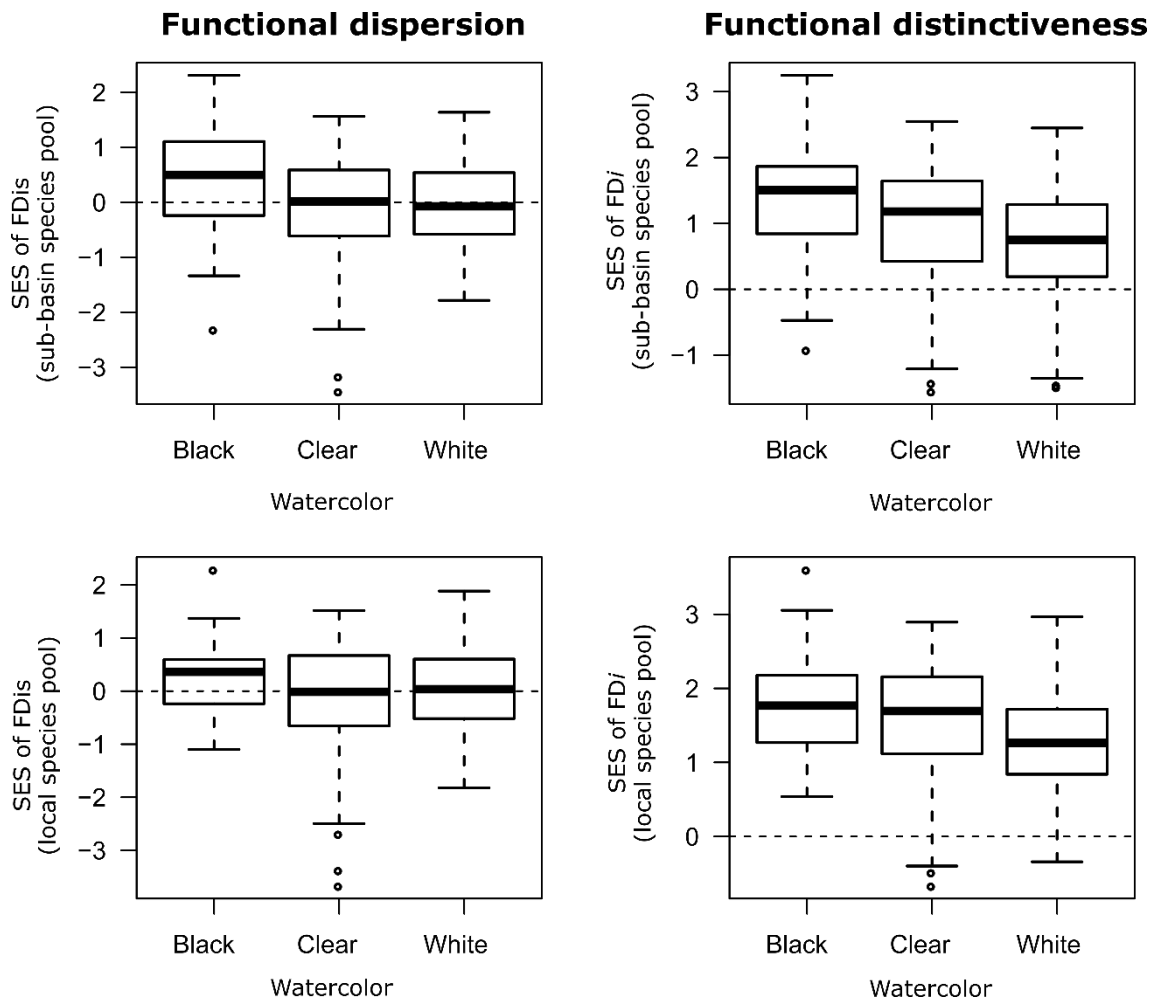
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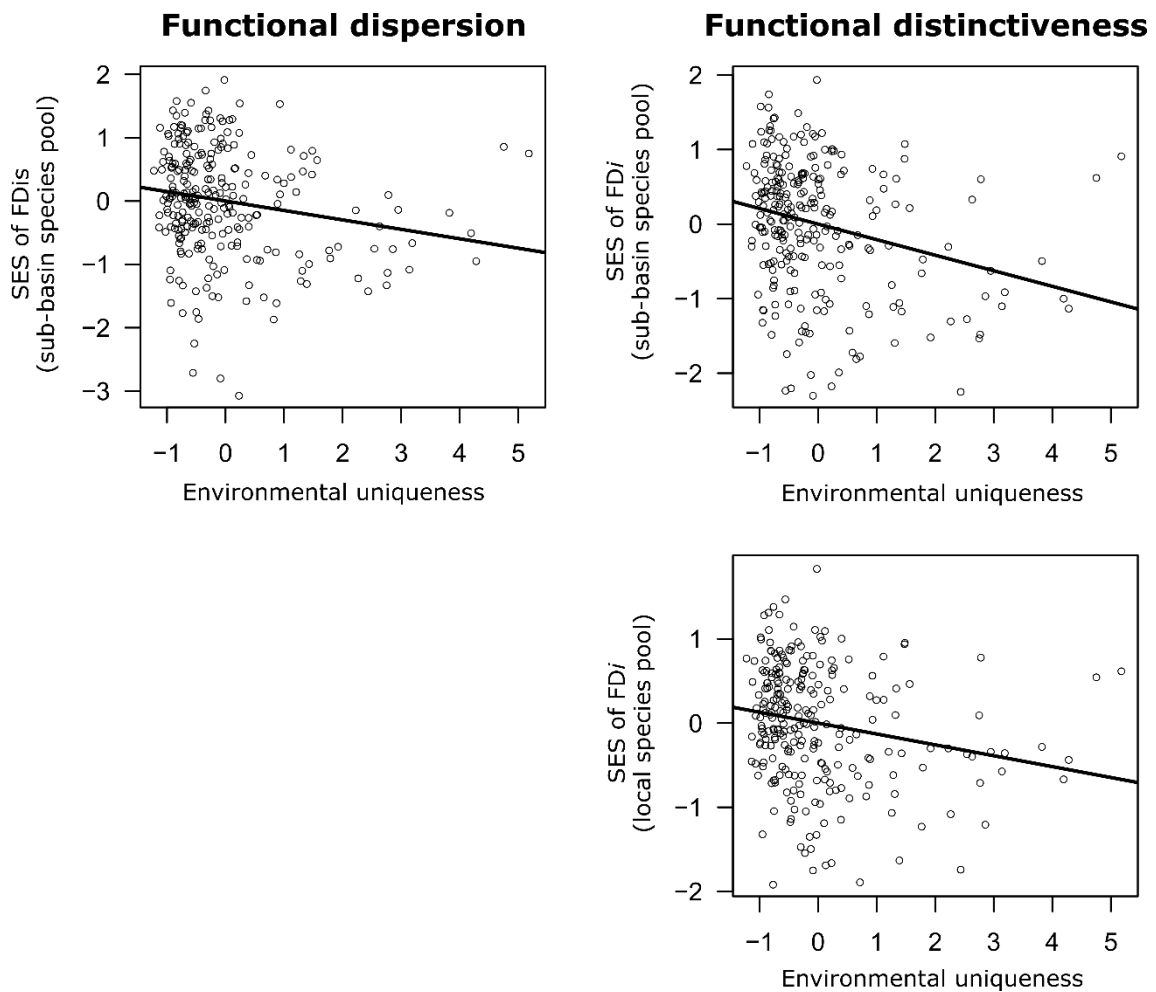
**Supporting information 4: Relationships between historical and ecological drivers and assembly patterns – trait underdispersion and overdispersion.**



**Figure S4.1** Effect of the marine incursions at ~5 Mya showing the significant relationship between this predictor and the SES values of functional dispersion (FDIs) and functional distinctiveness (FDi) under null models considering sub-basin and local species pool. (0) streams that have not been submerged from seawater; (1) streams that have been submerged from seawater. Please note that the trait underdispersion is predominant in negative values of the y-axis when using the sub-basin species pool in the null model. On the other, trait overdispersion is predominant in positive values of the y-axis when using the local species pool in the null model.



**Figure S4.2** Effect of the sub-basin watercolor marine incursions at ~5 Mya showing the significant relationship between this predictor and the SES values of functional dispersion (FDIs) and functional distinctiveness (FDi) under null models considering sub-basin and local species pool. Please note that the trait underdispersion is predominant in negative values of the y-axis when using the sub-basin species pool in the null model. On the other, trait overdispersion is predominant in positive values of the y-axis when using the local species pool in the null model.



**Figure S4.3** Effect of the sub-basin watercolor marine incursions at ~5 Mya showing the significant relationship between this predictor and the SES values of functional dispersion (FDi) and functional distinctiveness (FDi) under null models considering sub-basin and local species pool. Please note that the trait underdispersion is predominant in negative values of y-axis when using the sub-basin species pool in null model. On the other, trait overdispersion is predominant in positive values of y-axis when using the local species pool in null model.



**CAPÍTULO 3**

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Carlos Alberto de Sousa Rodrigues-Filho, Fabricio Beggiato Baccaro, Jansen Zuanon, Jorge Iván Sánchez-Botero, Ronaldo César Gurgel-Lourenço, Rafael Pereira Leitão. The functional structure of species pools explains idiosyncratic assembly patterns among biogeographical regions. Manuscrito em preparação para a revista *Freshwater Biology*.

**RESEARCH PAPER**

**Title: The functional structure of species pools explains idiosyncratic assembly patterns among biogeographical regions**

**Short title: Historical legacy drives idiosyncrasy**

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**Abstract**

**Aim:** Habitat features act as an environmental filter selecting organisms from regional species pools adapted to a set of particular conditions. This supposedly leads to predictable assembly patterns of local communities based on the relationship between functional traits and the environment. However, different functional composition has frequently been found even under similar conditions, suggesting that environmental filters may not work the same way across different biogeographic regions. We hypothesized that these inconsistencies might result from differences in the functional structure of the regional species pools, both in terms of diversity (SPFD<sub>diff</sub>) and compositional dissimilarity (SPF $\beta$ ).

**Location:** Amazon Basin and Brazilian Northeast streams.

**Taxon:** Neotropical stream fish.

**Methods:** We quantified the relationships between environment and functional structure across 107 stream fish assemblages from two Neotropical biomes (Amazonia and Caatinga) with drastic historical differences. First, we compared the species pools using null models and tested whether environmentally similar streams between the two regions tend to harbor assemblages with similar functional structures. Second, to explicitly test the effect of SPFD<sub>diff</sub> and SPF $\beta$  in the functional trait-environment relationship, we build an algorithm that resamples 10 streams in each biome (999 times) following specific rules that minimize the influence of spatial processes in the local functional composition.

**Results:** We found marked levels of in SPFD<sub>diff</sub> and SPF $\beta$  between Amazonia and Caatinga and a weak relationship between environmental and functional dissimilarity among assemblages. This result is better understood from the results of the balanced resampling. We demonstrated that the greater the differences in the functional structure of species pools between two regions (high SPFD<sub>diff</sub> and SPF $\beta$ ), the weaker the relationships between environmental and functional similarity among local communities.

**Main conclusions:** Our findings highlight the importance of the functional structure of regional species pools in understanding the trait-environment relationship in local communities when comparing different biogeographical regions.

**Keywords:** Functional biogeography, species pool, environmental filters, neotropics, stream fish

## 1 | Introduction

A key issue facing ecologists and biogeographers is identifying the generality of multiple processes that drive the assembly of biological communities across biogeographic regions (Catano et al., 2017; Chase, 2003; Qian & Ricklefs, 2012). In this context, local habitat features are a major factor supposedly responsible for generating consistent and repeated patterns across regions (Violle et al., 2014). This idea is supported by the assumption that habitat acts as an environmental filter, restricting the establishment of organisms based on their functional strategies for living in a given site (Kraft et al., 2015). Thus, if environmental filters are globally consistent, local communities' functional composition (i.e., mean trait values) should change with the environment regardless of geographic distance or evolutionary history. However, the generalization of this prediction has often been challenged. While several studies suggest that the functional composition of local communities respond to changes in the environment in a similar fashion between biogeographic regions (Cunico et al., 2011; Hemingson & Bellwood, 2018), others do not support this idea, revealing different functional compositions even under similar environmental conditions (Bender et al., 2013; Lamanna et al., 2014). Here, we argue that these idiosyncrasies are, at least in part, explained by historical processes, which result in different arsenal of functional traits that can be selected by local environmental filters in each biogeographic region.

The link between history and contemporary local-scale parameters may be understood from a hierarchical perspective. Historical events define the species pool available in a region from which species may (or may not) colonize local communities (Zobel, 1997). However, each region's history is unique, generating marked differences in species pools (Vellend, 2016). Consequently, the functional structure of the species pool (e.g., diversity and composition of functional traits) also changes between regions (Shipley, 2010). Given that functional traits reflect the ability of individuals to grow and reproduce in particular habitats (Violle et al., 2007), supposedly expressing deterministic processes (e.g., niche selection) (Saito et al., 2016), the functional structure of the species pool emerges as an important factor for understanding how the environmental filters can drive the differences in functional composition between local communities (i.e., functional dissimilarity) across biogeographical regions (Zobel, 2016). For example, nondeterministic historical processes may remove a set of species highly specialized to a particular habitat in one region but not in another, generating different functional compositions even under similar environmental conditions (Pärtel, 2002). Even so, most studies have assumed that environmental filters are globally consistent and generate predictable local community patterns among biogeographical regions (Hemingson & Bellwood, 2018; Lamouroux et al., 2002).

The functional structure of a regional species pool can be characterized by diversity and compositional components, representing the variability and type of functional traits available to be selected by local environments (Table 1). The species pool functional diversity (SPFD) expresses the extent of traits combinations regionally available to local filtering. So that, the higher the SPFD, the greater the likelihood of trait combinations that favor the occurrence of a given species at the particular environment (Chase, 2003), potentially generating fine-tuned adjustments between species traits and local habitat. On the other hand, the species pool functional composition expresses the most expected trait combinations regionally available to local filtering. These two components can be compared between

regions to provide a quantitative estimative of their differences in species pool functional structure. Species pool functional diversity differences (hereafter,  $SPFD_{diff}$ ) reflect the extent to which the SPFD of one region is greater than the other. In contrast, the difference in species pool functional composition (hereafter,  $SPF\beta$ ) reflects the dissimilarity in trait combinations between regions (Table 1).

These two complementary facets of species pool functional structure bring about interesting theoretical predictions regarding the consistency of environmental filters that yield similar functional patterns across evolutionarily distinct communities (Figure 1). More specifically, we argue that the species pool functional structure influences fundamental processes of local communities within regions (i.e., environmental filtering; Denelle et al., 2019), which in a biogeographical context should influence the consistency of the environmental filters in generating repeated ecological patterns. For example, when  $SPFD_{diff}$  and  $SPF\beta$  between two regions are low, a pair of sites of distinct regions with similar environmental filters would generate similar functional composition, while sites with different environmental conditions do not. In this scenario of high similarity of species pools, we expect a strong relationship between environmental and functional dissimilarity (Figure 1a). In contrast, higher  $SPFD_{diff}$  and  $SPF\beta$  among regions would lessen the predictability of environmental filters in yielding similar local functional structure. Hence, we would expect a weak relationship between environmental and functional dissimilarity among regions (Figure 1b, c).

Here, we investigated how the differences in species pool functional structure affect the consistency of the environmental filters in yielding the functional dissimilarity of local assemblages between two Neotropical biomes. As a study model, we used 107 headwater streams from Amazonia and Caatinga with marked regional differences in species composition but similar conditions in the current habitat structure (Rodrigues-Filho et al., 2018). We considered two analytical approaches. Initially, we tested the difference in the functional structure of fish species pools between Amazonia and Caatinga and whether the environmentally similar streams yield similar functional composition. Based on the marked historical differences between biomes, we expect the ichthyofauna of Amazonia and Caatinga to harbor different functional strategies (high  $SPFD_{diff}$  and  $SPF\beta$ ). Therefore, environmentally similar streams do not consistently yield similar functional compositions. Then, we carried out a resampling analysis coupled with null models to test whether the relationships between environmental and functional dissimilarity between regions are influenced by their differences in the species pool functional structure. We propose that the differences in species pool functional structure ( $SPFD_{diff}$  and  $SPF\beta$ ) affect the consistency of the environmental filters across biogeographical regions. The greater the  $SPFD_{diff}$  and  $SPF\beta$ , the weaker the relationship between environmental and functional dissimilarities.

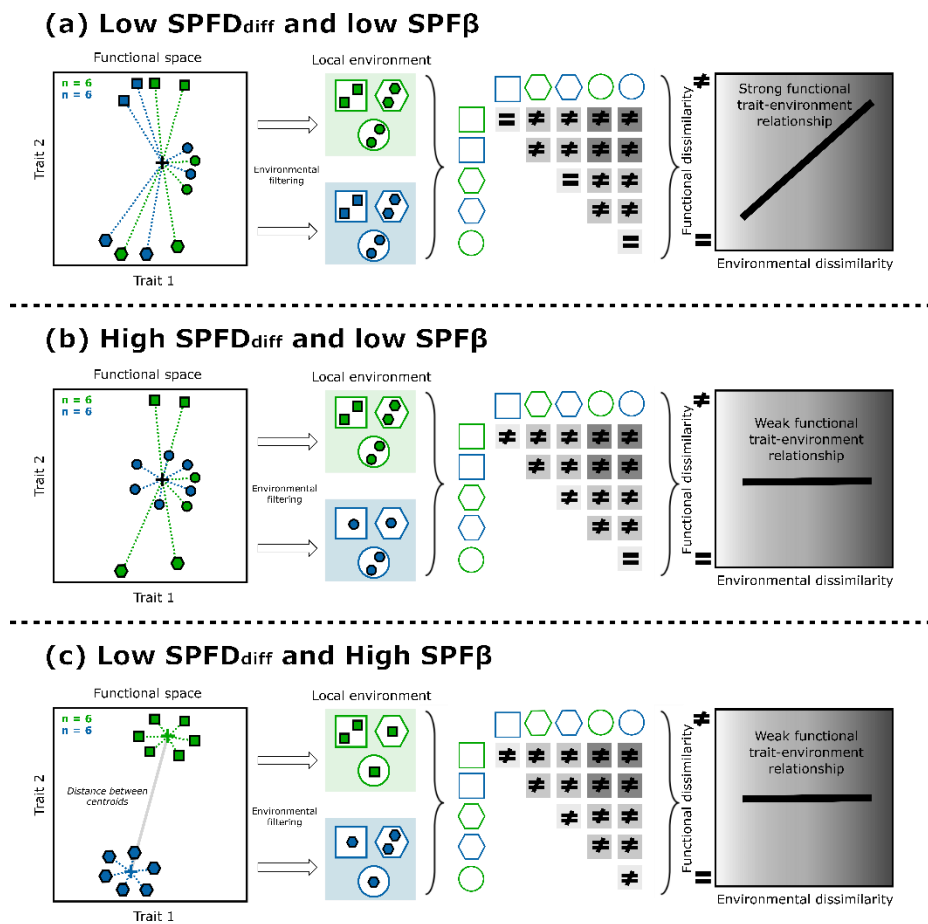


Figure 1. A conceptual framework linking the functional structure of two regional species pools (green and blue) and local communities by local environmental conditions. We provided three scenarios comparing two regional pools with identical number of species ( $n = 6$ ) but with different functional structure, in terms of diversity and composition of functional traits. Species are placed in a bidimensional functional space according to their functional traits, with similar symbols (squares, diamonds, or circles) representing their proximity in terms of functions. The species pool functional diversity ( $SPFD$ ) is expressed by the mean distance of each species to the centroid (crosses) of the functional space in each region, and then the difference in  $SPFD$  ( $SPFD_{diff}$ ) can be assessed by the ratio between regions. The compositional dissimilarity ( $SPF\beta$ ) can be measured by the distance between centroids of each region. In each local community, environmental filters select for a particular trait (fitting according to their respective symbol). Pairwise comparisons can reflect the environmental similarity (gray gradient) and the functional similarity (= for similar functional composition and  $\neq$  for different functional composition) among communities of the two regions. (a) When  $SPFD_{diff}$  and  $SPF\beta$  are low, similar environmental filters (light gray in association matrix) will lead to similar functional composition ( $=$ ), while different environmental filters (dark gray in association matrix) do not ( $\neq$ ), resulting in a positive relationship between environmental and functional dissimilarity. On the other hand, (b, c) high levels of  $SPFD_{diff}$  and  $SPF\beta$  may obscure local community patterns, enabling similar or different functional composition patterns regardless of the environmental similarity, and thus a weak relationship between environmental and functional dissimilarity should be expected. See detailed definitions of terms in Table 1.

Table 1. Glossary of the terminology used in this study.

Term	Definition
Species pool	The overall set of species in a region that could potentially co-occur in a site given the operating environmental and dispersal filters (Pärtel et al., 2011).
Functional space	A multidimensional space where the axes are functional trait values, or their synthetic reduction derived from multivariate analysis (e.g., PCA or PCoA), along which species are placed (Villéger et al., 2008).
Species pool functional diversity (SPFD)	The variability of functional traits in the regional species pool (Spasojevic et al., 2018), which can be measured by different functional indexes, such as functional dispersion (Laliberté & Legendre, 2010).
Species pool functional diversity difference (SPFD <sub>diff</sub> )	The ratio between the SPFD of two regions. SPFD <sub>diff</sub> reflects the extent to which one region is more functionally diverse than another. SPFD <sub>diff</sub> = 1 means that two regions hold a similar range of traits combinations in the species pool, whereas SPFD <sub>diff</sub> > 1 means that one region holds more trait diversity than another.
Species pool functional composition	The dominant trait values of the species pool within the functional space. The species pool functional composition refers to the abundance-weighted centroid of the species pool within the functional space.
Species pool functional composition dissimilarity (SPFβ)	Euclidean distance between the species pool functional composition of two regions. SPFβ = 0 means that two regions have an identical centroid position of the species pool within the functional space. The greater SPFβ is, the greater the distance between centroids, and thus the difference in functional composition between two regions.
Local functional composition	The dominant trait values of a given local community within the functional space, expressed by their abundance-weighted centroid.
Functional dissimilarity	Euclidean distance between the abundance-weighted centroid of two local communities.
Environmental filters	Set of habitat features that favor some functional traits over others. Thus, 'environmental filters' concern the influence of habitat features in restricting the establishment or persistence of organisms based on their functional traits (Kraft et al., 2015).

## 2 | Materials and methods

### 2.1 | Local assemblages from biomes with different historical trajectories

This study was based on standardized fish samplings of headwater streams (first to third order, *sensu* (Strahler, 1957) from two Neotropical biomes: Amazonia, where sample sites drain to tributaries of the middle-lower Amazon, Curuá-Uná and Madeira Basin (53 streams); and Caatinga, where sample sites drain to tributaries of the Jaguaribe, Coreaú and Metropolitan Basins in Northeastern Brazil (54 streams) (Figure S1.1). Since around five million years ago, Amazonia and Caatinga began to follow different climatic and biogeographical trajectories, directly influencing the diversification patterns at local and regional scales (Rodrigues-Filho et al., 2018). Because of this historical divergence, the functional structure of the regional species pool should differ between the biomes. However, many small streams show similar local environmental conditions (e.g., water velocity and substrate types). Therefore, we used this scenario to test how divergent historical processes influence the role of local environmental conditions in modulating the functional patterns of local fish assemblages when comparing different biogeographical regions.

Streams were sampled between 2011 and 2016 following the same standard protocol for both regions (Mendonça et al., 2005); see Appendix S1 in Supporting Information). We measured local

environmental conditions in each stream site (50-m long stretch), including channel depth and width, water velocity, canopy cover, macrophyte, substrate composition, and temperature. All sampling sites are located at altitudes from near zero to 500 m a.s.l. Depth (m) and width (m) was measured with a ruler and measuring tape, and velocity (m/s) was estimated by the time necessary for a floating object to cover a known linear distance along the main channel. Macrophyte was also treated as 0 or 1 to characterize streams with and without macrophyte presence, respectively. The relative substrate composition (%) was visually classified in eight categories: pebble/gravel (1-10 mm in diameter), sand (0.1-1 mm), clay (0.05-0.1 mm), trunk (> 10 cm), litter (dead leaves and small branches), and fine litter (organic detritus). Temperature (°C) was measured with *Hanna HI9146* instrument exactly downstream from the 50-m stretch. These local environmental conditions are often considered the main drivers structuring fish assemblages at local scales (Hoeinghaus et al., 2007; Rodrigues-Filho et al., 2017). Although thousands of kilometers separate sampled streams, some of them present strong environmental similarities (Figure S1.2). After environmental characterization, fishes were caught during daylight hour with sieve and seine nets, euthanized by immersion in an anesthetic solution of Eugenol, fixed in 10% formalin, and later preserved in 70% alcohol. Voucher specimens are deposited in the Fish Collection of National Institute for Amazonian Research (INPA, Manaus) and Federal University of Rio Grande do Norte (UFRN, Natal).

## 2.2 | *Building of the functional space*

To describe the functional structure of the regional species pools and the local fish assemblages, we first conducted an ecomorphological analysis based on a set of morphometric data collected from 3-10 adult individuals of each species. Combinations of these measures generated 15 functional traits related to locomotion capacity, food acquisition, and water-column occupation (for details, see Appendix S2 in Supporting Information). Although representing only a portion of the total amount of functional roles (Winemiller et al. 2015), ecomorphological traits are recognized as a valid proxy for crucial functions performed by fish (Villéger et al., 2017) and have been successfully used for assessing the relationship between species and environmental conditions in streams (Bower & Winemiller, 2019). The main advantage of these traits is their easy mensuration among all species in different biogeographical regions (Lamouroux et al., 2002; Toussaint et al., 2016). This is especially important when researching megadiverse regions, such as the Amazon (Dagosta & Pinna, 2019), and in those from which basic ecological information of species is lacking (e.g., life history, habitat use, trophic and behavioral aspects).

To construct the multidimensional functional space (Table 1), we centered to zero mean and unit standard deviation the 15 ecomorphological traits. Subsequently, a principal component analysis (PCA) was performed to reduce dimensionality and plot the species according to their traits (Villéger et al., 2008). Based on the protocol developed by (Maire et al., 2015) to determine the number of axes that guarantee a high-quality functional space, we used the first four PCA axes (65.9% of explained variance). We quantified the functional indices for regional (between biomes) and local scale (among local assemblages) based on this four-dimensional space.

## 2.3 | *Regional and local functional structures of fish assemblages*



Within each biome, the species pool functional diversity (SPFD) represents the mean abundance-weighted distance of all species to the centroid of the species pool (FDis; (Laliberté & Legendre, 2010); Table 1). This index has the advantage of being independent of regional species richness allowing a fair comparison between regions (e.g., Amazonia and Caatinga). We then quantified the difference in species pool functional diversity (SPFD<sub>diff</sub>) between biomes following the equation:

$$SPFD_{diff} = \left| \frac{SPFD_{region1}}{SPFD_{region2}} \right|$$

The species pool functional composition was calculated as the position of the abundance-weighted centroid of the biome in the functional space (Mouillot et al., 2013). We then calculated the Euclidean distances between the centroids of Amazonia and Caatinga to obtain their species pool functional dissimilarity (SPF $\beta$ ; Table 1). Similarly, we quantified the abundance-weighted centroid to each local assemblage and then calculate their pairwise Euclidean distances to quantify the functional dissimilarity matrix (Table 1). Both FDis and abundance-weighted centroid were quantified from the function *multidimFD*, available on Villéger's website (<http://villeger.sebastien.free.fr/Rscripts.html>).

#### 2.4 | Data analysis

To estimate sampling completeness, we estimated the extrapolated species richness in a species pool for each biome and inspected their species accumulation curves. For this, we used the R functions *specpool* and *poolaccum* from the package 'vegan' (Oksanen et al., 2013). Four incidence-based estimations were used: Chao, Jackknife (first and second order), and bootstrap.

##### 2.4.1 | Species pool functional structure differences between Amazonia and Caatinga

To test whether the differences of the species pool functional structure between Amazonia and Caatinga biomes were significantly different from random, we carried a null model that shuffled the species composition while maintaining the species richness and occurrence in each biome. The differences in species pool functional diversity (SPFD<sub>diff</sub>) and composition (SPF $\beta$ ) were then calculated for every 999 iterations. For both SPFD<sub>diff</sub> and SPF $\beta$ , p-values were computed by comparing observed values to the distribution of simulated values. Significant differences between biomes were assumed when the observed values differed from 95% of the null distribution of the expected values.

##### 2.4.2 | Importance of environmental filter in explaining the trait composition in Amazonia and Caatinga

We used a partial multiple regression based on distance matrices (MRM) to verify whether environmental dissimilarity (Euclidean distance between streams) predicts the functional dissimilarity between fish assemblages from Amazonia and Caatinga, using biome identity as a covariable. The slope of this relationship was used as a proxy of the strength of environmental filtering in the assembly of local communities. If the slope was nonrandom and positive, we assumed that environmental filtering is strong enough to define the functional dissimilarity among fish assemblages from Amazonia and Caatinga. On the other hand, if the slope was random and close to zero, we assumed that the environmental filtering is weak. Therefore, the functional dissimilarity among fish assemblages from Amazonia and Caatinga is not defined by the local habitat.

We compared the observed slope to those expected under a null model that removed any associations between species traits and local environmental conditions to test the slope randomness. To do that, we build random local communities within each biome, preserving their species richness and frequency of occurrence by using the *independentswap* algorithm of the package ‘picante’ (Kembel & Kembel, 2020). We repeated these processes 999 times. In each repetition, we recalculated the functional dissimilarity among assemblages and reexamined the relationship between functional and environmental dissimilarity to develop null distributions of simulated slopes. If the observed slope is greater than the 95% of simulated slopes, we assumed that the environmental filtering is stronger than expected by chance. Therefore, environmentally similar sites between Amazonia and Caatinga tend to have similar functional compositions. In contrast, we assumed weak environmental filtering if the observed slope is inside the 95% interval of the simulated slopes.

#### *2.4.3 | Importance of the differences in species pool functional structure to local selection between regions*

Testing the influence of historical processes in local processes based on niche (e.g., environmental filtering) across biogeographical regions using observational data is prone to error when it is made using data sets with different spatial configurations (Myers et al., 2013). Specifically, in aquatic ecosystems, spatial extent and sub-basin identity are considered important spatial factors able to influence the functional composition of local communities (Leibold & Chase, 2017; Oberdorff et al., 2019). As such, to explicitly test the influence of the differences in species pool functional structure to the relationships between environmental and functional composition across communities from different regions is necessary to control the spatial configuration. To do that, we built a parameterized balanced resampling coupled with a null model (Arellano et al., 2016; Tello & Stevens, 2010).

The parameterized balanced resampling selects 10 streams in each biome 1,000 times (Figure 2a). However, this selection was not completely random. Instead, we build an algorithm to guarantee that in each round, all streams are draining to the same sub-basin (see Figure S1.1) and ranging from 50 to 250 km<sup>2</sup>. This small spatial extent guarantee that dispersal limitation is sufficient to allow individuals to reach sites that match their functional traits (Leibold & Chase, 2017) and therefore favor the action of environmental filters. Thus, in our resamples, the relationship between environmental and functional dissimilarity is barely affected by dispersal limitation. Our algorithm also minimizes the overlap between rounds in terms of stream identity so that no round shares more than 70% of its stream’s identity with another round. This step avoids similar comparisons are made. Finally, all sub-basins were equally retained in each round to guarantee that the whole spatial scales inside each biome have been used and hence avoiding that a sub-basin with high density of streams dominates the final model. Further details about the rules are provided in Appendix 3, and the R script used to run the balanced resampling.

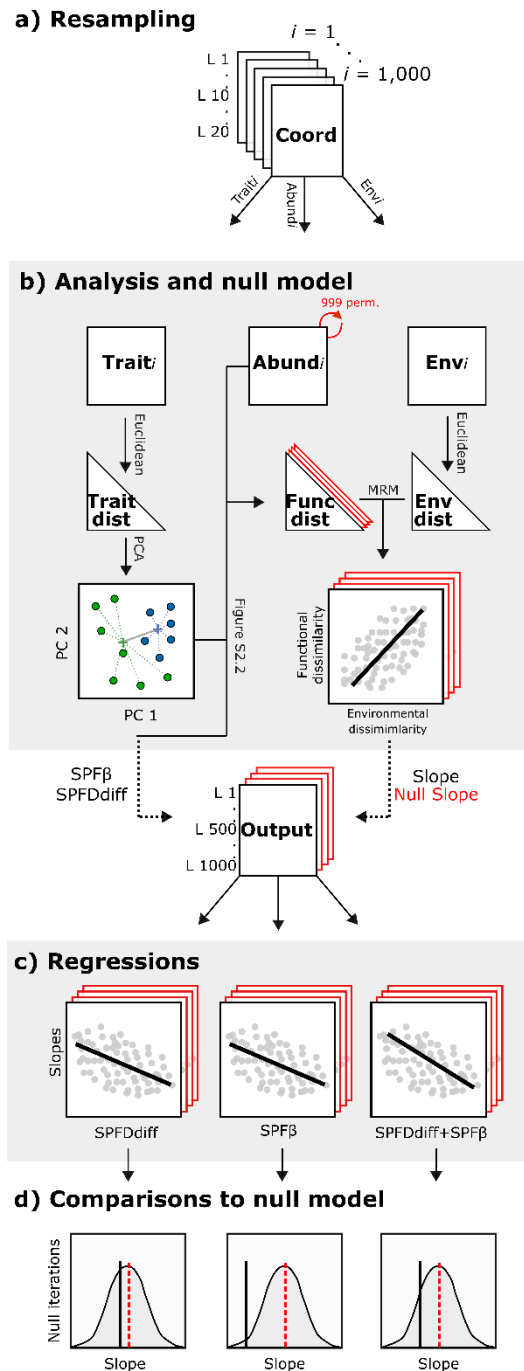


Figure 2. Balanced resampling and null model workflow used to test the importance of the species pool functional diversity difference (SPFD<sub>diff</sub>) and species pool functional composition dissimilarity (SPF $\beta$ ) (Table 1) in modulating the relationships between the environmental and functional composition of local communities when comparing different biogeographical regions. (a) 1,000 resampled matrices were built following specific rules to guarantee similar spatial extent (area in km<sup>2</sup> calculated from a matrix of spatial coordinates; Coord) and coverage of sites distribution within each biome (see Appendix 4). (b) for each of the 1,000 matrices, we calculated the slope between environmental and functional dissimilarity using a partial MRM analysis, keeping biome identity as a covariable, and quantified the differences in the species pool functional structure (i.e., SPFD<sub>diff</sub> and SPF $\beta$ ) between regions. In addition, for each resample, we generated 999 null communities to obtain the expected relationship between environmental and functional

dissimilarity. (c) linear regressions between the observed slope values and  $SPFD_{diff}$  and  $SPF\beta$ . (d) comparisons between the observed slope and those obtained from null communities. Env – stream environment conditions; Trait – species trait; Abund – species abundance.

In each resample round, we had three matrices with 20 rows each (10 sites per biome): species traits, species composition, and local environmental variables. Based on these matrices, we ran the partial MRM analysis to account for the relationships between environmental and functional dissimilarity. Using the species traits and species composition, we quantified the differences in the functional structure of the species pool:  $SPFD_{diff}$  and  $SPF\beta$  (see Figure S2.2 for more details). Here, we assumed that the species pool in each biome was composed by the sum of species present in the 10 streams by assuming that these species encompass the subset of species able to persist in these streams' environments (Bernard-Verdier et al., 2012; Münkemüller et al., 2020). In addition, we also estimated the species pool considering the locally absent species (Supporting information 4), but the main results did not change (Table S6.1). Thus, for simplicity, we show only the results based on the species pool obtained from the species present in the 10 streams. After carrying these steps for each round, we obtained an output with 1,000 rows and three columns (i.e., slope,  $SPFD_{diff}$ , and  $SPF\beta$ ) (Figure 2b).

Using the output data, we fitted linear regressions using the slopes as response variables and all the three combinations of  $SPFD_{diff}$  and  $SPF\beta$  (e.g., only  $SPFD_{diff}$ , only  $SPF\beta$ , and  $SPFD_{diff} + SPF\beta$ ; Figure 2c). The model's quality was assessed by visual inspection of residuals plotted against fitted values (Figures S6.1 and S6.2). We then calculated the Akaike information criteria corrected for sample size (AICc) for each model. Delta AICc ( $\Delta AICc$ ) and Akaike model weights ( $\omega AICc$ ) were calculated from AICc values to detect the best model using the function *aictab* with the package 'AICcmodavg' (Mazerolle & Mazerolle, 2017). Finally, to test the significance of these relations, we compare the observed regression slopes to the slopes obtained by fitting similar regressions models using expected slopes values from the null model described above (red squares and triangles in Figure 2b, c). This procedure was carried out 999 times per resampling round using the "independentswap" algorithm to permute the species composition matrix. We considered a regression slope statistically significant if it differed from 95% of the null distribution coefficients, suggesting that either  $SPFD_{diff}$  or  $SPF\beta$  significantly influence the strength of environmental filters between regions.

### 3 | Results

A total of 183 fish species distributed in six orders were collected from Amazonia (140 species) and Caatinga (46 species) (Supporting Information 7). These values were close to expected in both Amazonia (64% - 88%) and Caatinga (79% - 90%) (accumulation curves are available in Appendix S5). The species composition was strikingly different between Amazonia and Caatinga with only three species present in both biomes (~1.6% of taxonomic similarity). On average, the stream sites supported 11 species (standard deviation = 8.8) and 6 species (standard deviation = 3.0) in Amazonia and Caatinga, respectively.

#### 3.1 | From species pool functional structure to the local assemblages

We found a striking difference in species pool functional structure, both calculated by  $SPFD_{diff}$  and  $SPF\beta$ , between Amazonia and Caatinga. Overall, Amazonian species predominantly occupy the outer portion of the functional space (Figure 3), with the regional pool having approximately 50% more functional diversity than Caatinga. This observed difference in species pool functional diversity significantly differ from random ( $SPFD_{diff} = 1.5$ ; mean of  $SPFD_{diff}$  null distribution = 1.19, 95% = 1.33;  $p < 0.001$ ). The dominant trait combination also significantly differs between biomes ( $SPF\beta = 1.77$ ; mean of  $SPF\beta$  null distribution = 0.63, 95% = 0.92;  $p < 0.001$ ). These differences are largely due to differences in PC 2 to PC 4, which are correlated with functional traits related to locomotion and habitat exploration (Figure 3).

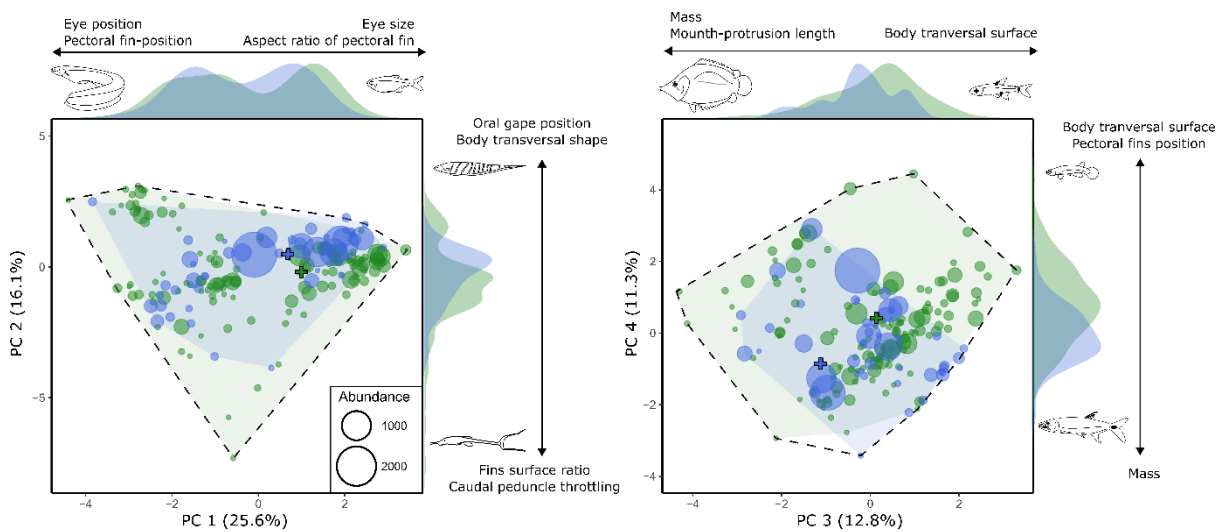


Figure 3. Functional space occupied by stream fish species based on the first four principal component axes for the Amazonia (green) and Caatinga (blue). Dots correspond to each species, with size proportional to their abundance in each biome. The abundance weighted centroid of each biome is represented by crosses. The convex hull of all species pool (dotted lines) and for Amazonia (green polygons) and Caatinga (blue polygons) were delimited to visually examine how the species were distributed according to their trait's combinations. Fish illustrations (not drawn to scale) demonstrate the main ecomorphotypes that characterize the ecomorphological traits at the end of the arrows (see Table S2.2). The curves following the PC axes represent the density estimates of the species distribution along each one.

We found a positive, although weak, relationship between environmental and functional dissimilarity among stream fish assemblages from Amazonia and Caatinga ( $R^2 = 0.4\%$ ; slope = 0.03; Figure 4a). This relationship was not greater than expected by chance ( $p = 0.13$ ; Figure 4b).

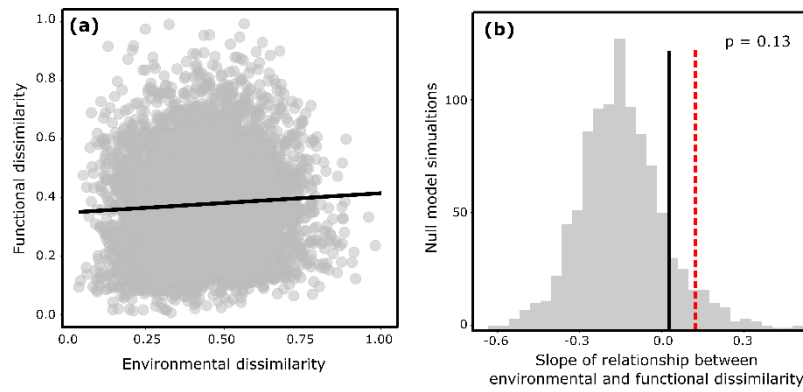


Figure 4. Relationship between environmental and functional dissimilarity of 107 local fish assemblages from Amazonia and Caatinga (a), and results from null model analysis (b). Histogram shows expected slopes from 999 simulations that preserved the observed local species richness and frequency of occurrence. The dashed red line shows the 95% quantile of the expected slope from the null model, while the solid black line shows the observed slope.

### 3.2 | Influence of the difference in species pool functional structure on the functional trait-environment relationships

We found support for the model that includes the effects of both  $SPFD_{diff}$  and  $SPF\beta$  in explaining the slope of the relationship between environmental and functional dissimilarity ( $\Delta AICc < 2$ ; Table 2). As expected, the strength of environmental filtering in predict similar functional composition decreases with both  $SPFD_{diff}$  (slope = -0.08;  $p = 0.01$ ) and  $SPF\beta$  (slope = -0.13;  $p < 0.01$ ). In other words, significant relationships between environmental and functional dissimilarity are more prone to be detected when comparing regional species pools with similar functional structures (low  $SPFD_{diff}$  and  $SPF\beta$ ; letter “a” in Figure 5). In contrast, marked differences in the species pool functional structure (high  $SPFD_{diff}$  and  $SPF\beta$ ) change the expected outcome of environmental filtering between regions. Hence, weak, and close to zero relationships between environmental and functional dissimilarities are observed (letter “b” in Figure 5). These relationships significantly differed from null expectations (Table 2).

Table 2. Hierarchical models used to determine under which conditions species pool functional diversity difference ( $SPFD_{diff}$ ) and species pool functional composition dissimilarity ( $SPF\beta$ ) is most likely to influence the strength of environmental filtering among stream fish assemblages from Amazonia and Caatinga (slopes of MRM analysis, using functional dissimilarity as the response variable and environmental dissimilarity as a predictor variable). The best-ranked model is shown in bold. (\*) represents significantly slopes in comparison with the null model.

Models	Intercept	$\beta$ Parameter		Akaike information		
		$SPFD_{diff}$	$SPF\beta$	AICc	$\Delta AICc$	$\omega AICc$
<b>slope ~ <math>SPFD_{diff}</math> + <math>SPF\beta</math></b>	<b>0.23</b>	<b>-0.08*</b>	<b>-0.13*</b>	<b>-1875.5</b>	<b>0.00</b>	<b>1.00</b>
slope ~ $SPF\beta$	0.10		-0.13*	-1829.5	46.06	0.00
slope ~ $SPFD_{diff}$	0.16	-0.07*		-1822.8	52.71	0.00
slope ~ Intercept	0.04			-1783.7	91.84	0.00

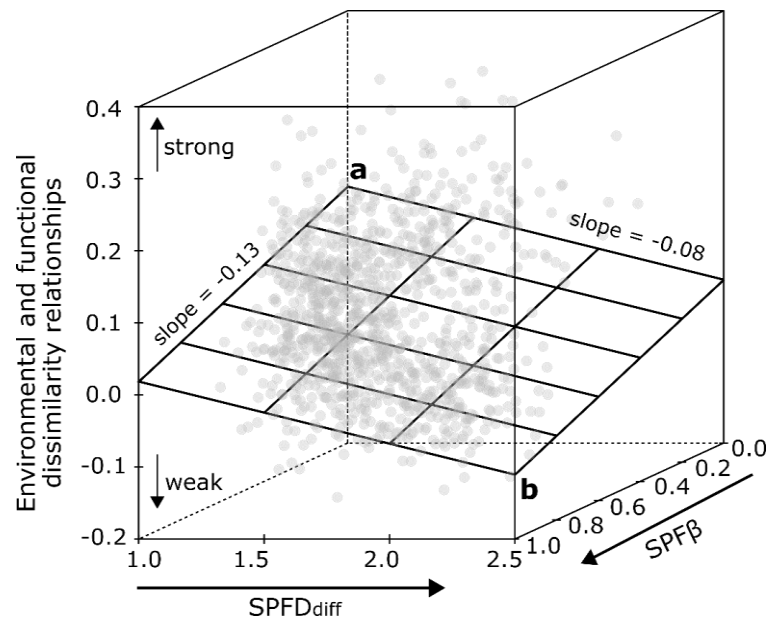


Figure 5. Relation between species pool functional diversity difference ( $SPFD_{diff}$ ), species pool functional composition dissimilarity ( $SPF\beta$ ), and the environmental and functional dissimilarity relationships (slopes of partial MRM analysis) of 1,000 resamples from fish assemblages of Amazonia and Caatinga (gray points). Letters indicate parts of the graph cited in the Results and Discussion sections.

#### 4 | Discussion

Accurately predicting the functional composition of local communities based on local environmental conditions would help in elucidating how assembly mechanisms operate, as well as in subsidizing better conservation policies to address the growing effects of multiple global changes in the Anthropocene (Hortal et al., 2012; McLean et al., 2019). However, the huge number of factors that may govern the local community patterns have precluded a comprehensive general framework from addressing this question (Lessard et al., 2012). Despite the many possible mechanisms (Chase & Myers, 2011; Lessard et al., 2012), here we provide empirical evidence that the differences in species pool functional structure can be used to elucidate when environmental filters are prone to generate consistent functional patterns across communities from different biogeographical regions. Overall, we showed that similar local environmental conditions do not predict the functional-trait composition of stream fish assemblages from two Neotropical biomes with contrasting evolutionary history and species pool functional structures. This pattern can be more deeply understood from the results of the balanced resampling. Specifically, the greater the difference in the species pool functional structure between regions, the lower our capacity to predict the functional composition of local communities based solely on environmental conditions. Thus, instead of emphasizing whether environmental filtering generate consistent patterns between regions (Weiher et al., 2011), we stress that more attention should be devoted to how the differences in the functional structure of the species pool modulate the local processes based on niche selection (Spasojevic et al., 2018).

##### 4.1 | Functional composition–environment relationships across Amazonia and Caatinga

Moving in the water implies strictly respecting the physical hydrodynamic laws, and morphotypes not adapted to current flows pay higher energetic costs to perform basic ecological functions such as locomotion and foraging (Gatz, 1979). This has led to the formulation of theories assuming that physical habitat characteristics accurately predict the functional trait combinations of aquatic organisms across different biogeographical regions (Poff, 1997). To test this hypothesis, we compared the functional composition of fish assemblages between streams from Amazonia and Caatinga, two Neotropical biomes largely distinct in terms of evolutionary history. Considering physical limitations imposed by water drag, stream ecosystems were expected to strongly prefer fish morphologies based on a set of ecomorphological traits (Bower and Winemiller 2019; Leitão et al. 2018). In striking contrast, however, we registered low importance of stream environmental conditions on explain the functional composition of fish assemblages of Amazonia and Caatinga. Essentially, it appears that the ecomorphological structures of fish assemblages were different regardless of local environmental filters, thereby according to the idea that differences in evolutionary history of between regions can temper the expected consistent action of environmental filters across regions.

Historical processes shape the diversity and composition of regional species pools at long-time scales (Vellend, 2010). Nevertheless, little is known on how the species pool functional structure changes between biogeographical regions. Here the historical differences related to climatic stability appear as a possible candidate to explain the distinct species pool functional structure of the ichthyofauna from Amazonia and Caatinga (Rodrigues-Filho et al., 2018). Although being spatially close biomes and having a similar overall proportion of species per taxonomic family (Hubert & Renno, 2006), the unique historical processes experienced by each of them led to a high degree of regional functional differentiation in terms of variability and composition. Since the Plio-Pleistocene (~2 million years ago), the Caatinga biome has experienced repeated and strong environmental disturbances (e.g., marine incursions and climatic changes) (Pôrto et al., 2004), which are likely to explain the low functional diversity available in their species pool ichthyofauna in comparison to Amazonia. In contrast, the relative climatic stability may have favored the maintenance of high levels of species richness (Oberdorff et al., 2019) and the accumulation of a greater diversity of trait combinations in Amazonia. We also found that these historical differences have led to regional differences in species pool functional composition (SPF $\beta$ ). Thus, similar habitat types should be occupied by morphologically different fish in streams from Amazonia and Caatinga. For example, large-bodied species adapted to more structurally complex (i.e., macrophytes) environments are more frequent in Amazonia (negative score in PC 3 and PC 4 in Figures 3b), suggesting that such morphotypes could have been filtered out from the Caatinga streams. Similarly, elongated species adapted to explore submerged logs and sticks, aquatic vegetation or root tangles were predominant in Amazonia (negative scores in PC 1; Figure 3). Only one exemplary with this body shape was found in Caatinga (*Synbranchus marmoratus*).

#### 4.2 | Assemblage idiosyncrasies are more common when the functional structure of species pools differs

Understanding the mechanisms underlying the idiosyncratic responses of biological communities to environmental conditions between biogeographical regions has been an important focus in ecology and biogeography (Lessard et al., 2012; Wiens & Donoghue, 2004). Idiosyncratic responses undermine our



capacity to predict how future environmental changes might modify the structure of local communities. This difficulty is partially promoted by the complex interactions between local processes and regional species pools (Jiménez-Alfaro et al., 2018). Two regions with similar species richness could have different trait combinations (Figure 1), which should have important consequences in local processes related with niche selection. The functional component of the species pool has been recently incorporated in ecological studies, revealing an important effect in local processes within and between biogeographical regions (Bennett & Pärtel, 2021; Denelle et al., 2019; Patrick & Brown, 2018). In accordance, we demonstrated how the differences in species pool functional structure can guide our expectations about when the environmental filters should yield similar functional composition across assemblages from different regions. Essentially, environmental filtering does not lead to generalized patterns of local community functional structure between regions with substantial differences in species pool functional structure (SPFD<sub>diff</sub> and SPFB). Together with other empirical evidence (Ernst et al., 2012; Forrestel et al., 2017; Van de Perre et al., 2020), the results of our resampling analysis fall in line with the fact that considering the consequences of historical processes is crucial for understanding the local assembly processes.

Environmental filters are often viewed as a strong deterministic process responsible for defining the functional composition of local assemblages, mitigating the interference of the differences in taxonomic identity of species pool between regions (Hoeinghaus et al., 2007). This assumption has led to the formulation of robust ecological hypothesis such as the “periodic table of niches” (Winemiller et al., 2015), which posits that predictable community patterns should arise in response to similar environmental conditions through consistent responses to environmental filtering. Nevertheless, some empirical findings have prevented the consolidation of this hypothesis, indicating that the link between local functional composition and environmental variables should not be assumed in all cases. Consequently, there is a debate about the generalization (or not) of the periodic table of niches, as well as related hypotheses (habitat template; (Townsend & Hildrew, 1994)). However, if we continue discussing the consistency of the environmental filter’s actions across regions under a dichotomic perspective – are they promoting consistent patterns or not? –, the more we will feed the context-dependency in ecology and biogeography (*sensu* (Lawton, 1999)). More than that, we defend that the differences in historical processes should complement local processes, such as environmental filtering, between regions. Still, this historical control could be investigated from the differences in species pool functional structure to provide more specific ecological predictions regarding the consistency of environmental filters in defining equivalent local patterns between regions, possibly leading to important implications for future theoretical formulations in ecological studies.

If historical processes promote differences in the taxonomic composition of species pools between regions, but the dissimilarity between their functional structures is small (i.e., low SPFB), the existence of similar environmental conditions would tend to generate a similar functional composition. This can be observed by analyzing assemblages from regions with a long period of geographical separation, such as the desert lizard assemblages in the United States and Australia, which demonstrate a strong level of similarity in habitat use even with drastically different taxonomic compositions (Melville

et al., 2006). The higher diversification rates of functional groups are mainly explained by the amount of evolutionary time, allowing species from different clades to have similar habitat exploitation ranges (Li & Wiens, 2019). A fascinating example of strong convergences between phylogenetically distant species is also observable for troglobitic species (e.g., cave Diplopoda), with congruent responses of some functional traits related to the exploration of subterranean environments around the world (e.g., body color and elongation of the tarsi of walking legs) (Liu et al., 2017). In opposition, the different historical events throughout the evolutionary frames in South America since 2 million years ago have precluded a consistent exploration of habitats for stream fish from different biomes. This set of evidence implies that, when predicting the role of environment filters between regions, it is necessary to consider their historical/evolutionary trajectories.

## 5 | Conclusions

Our study focused on how local environmental conditions define fish assemblages' functional structures in two South American biomes that had experienced different historical trajectories and have different species pool functional diversity and composition profiles. We found that considering the species pool functional structure concept in the analyses increases our capacity to accurately predict relationships between environmental filters and local functional composition across assemblages of different biogeographical regions. Specifically, we suggest that the hypothesis such as the 'habitat template' (Townsend & Hildrew, 1994) and the 'periodic table of niche' (Winemiller et al., 2015) can result in more consistent results when the species pool functional composition and diversity are more similar between biogeographical regions. Thus, it becomes necessary to use integrative approaches that consider the differences in species pool functional structure information for accurately predicting functional composition–environment relationships between biogeographical regions.

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## SUPPORTING INFORMATION

The functional structure of species pools explains idiosyncratic assembly patterns among biogeographical regions

Supporting information 1 – Streams geographical distributions and environmental similarity



Figure S3.1 Geographical locations of sampled streams sites in Brazilian Amazonia, where sample sites drain to tributaries of the middle-lower Amazon, Curuá-Uná and Madeira Basin (green area;  $n = 53$ ) and Caatinga biome, where sample sites drain to tributaries of the Jaguaribe, Coreaú and Metropolitan Basins in Northeastern Brazil (blue area;  $n = 54$ ). Points in the right and left plots represent the streams.

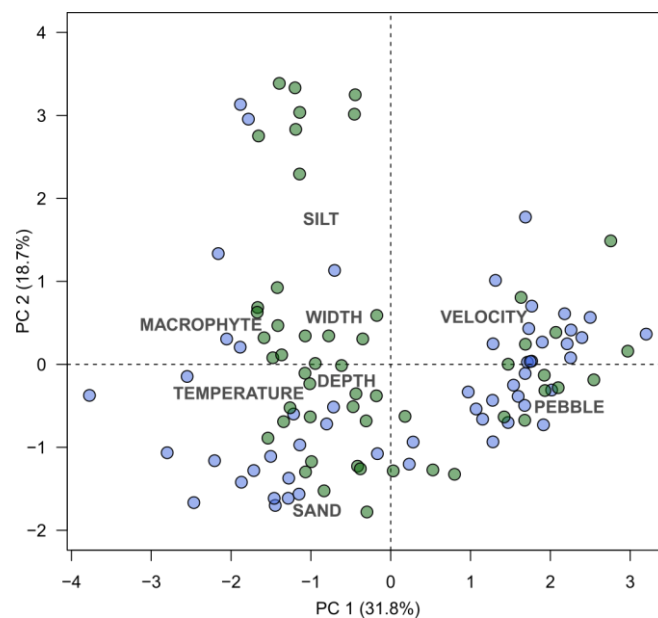


Figure S1.2 Principal component analysis (PCA) based on local habitat metrics to visualize the environmental similarity among 107 streams from Amazonia (green) and Caatinga (blue) biomes.



## Supporting information 2: Functional trait assessment

From the ecomorphological analysis (17 measures; Figure S2.1) and body mass (taken from a digital balance with an accuracy of 0.001g), we obtained 15 functional traits (Table S2.1) related to locomotion capacity, food acquisition and water column occupation for 183 fish species (according to Leitão et al., 2016). These measures were taken from 3-10 individuals per species. We used the mean values of each trait measured (see Table S2.1) among individuals of each species.

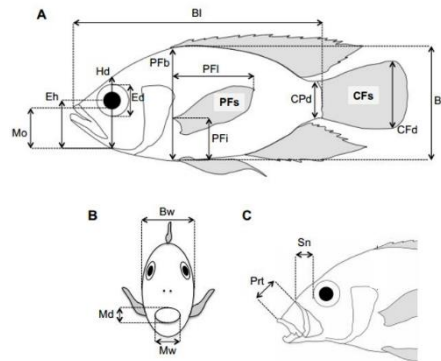


Figure S2.1 Seventeen morphological traits measured for fish on digital pictures (A): *Bd* body depth, *CPd* caudal-peduncle minimal depth, *CFd* caudal-fin maximum depth, *CFs* caudal-fin surface, *Cpd* caudal fin-depth, *PFI* distance between the insertion of pectoral fin to the bottom of the body, *Pfb* body depth at the level of the pectoral-fin insertion, *Pfl* pectoral-fin length, *Pfs* pectoral-fin surface, *Hd* head depth along the vertical axis of the eye, *Ed* eye diameter, *Eh* distance between the center of the eye to the bottom of the head, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis; and with digital caliper (B, C): *Bw* body width, *Md* mouth depth, *Mw* mouth width, *Sn* snout length, *Prt* protrusion length.

Table S2.1 List of 15 functional traits measured from the ecomorphological measurements of the fish species, with their ecological meanings. Adapted from Leitão et al. (2016).

Functional traits	Calculation	Abbreviation	Ecological meaning	References
Mouth-protrusion length	$\frac{Prt}{Sn}$	Prt	Feeding method	Adapted from Gatz (1979)
Oral-gape surface	$\frac{Mw * Md}{Bw * Bd}$	Osf	Size of food items captured	Adapted from Karpouzi & Stergiou (2003)
Oral-gape shape	$\frac{Md}{Mw}$	Osh	Method to capture food items	Karpouzi & Stergiou (2003)
Oral-gape position	$\frac{Mo}{Hd}$	Ops	Feeding method in the water column	Adapted from Sibbing & Nagelkerke (2001)
Eye size	$\frac{Ed}{Hd}$	Edst	Prey detection	Adapted from Boyle & Horn (2006)
Eye position	$\frac{Eh}{Hd}$	Eps	Vertical position in the water column	Gatz (1979)
Body transversal shape	$\frac{Bd}{Bw}$	Bsh	Vertical position in the water column and hydrodynamism	Sibbing & Nagelkerke (2001)

Body transversal surface	$\frac{\ln[(\frac{\pi}{4} * Bw * Bd) + 1]}{\ln(Mass + 1)}$	Bsf	Mass distribution along the body for hydrodynamism	Villéger <i>et al.</i> , 2010
Pectoral-fin position	$\frac{PFI}{PFb}$	PFps	Pectoral fin use for maneuverability	Dumay <i>et al.</i> , (2004)
Aspect ratio of the pectoral fin	$\frac{PFl^2}{PFs}$	FPar	Pectoral fin use for propulsion	Adapted from Fulton <i>et al.</i> , (2001)
Caudal-peduncle throttling	$\frac{CFd}{CPd}$	Cpt	Caudal propulsion efficiency through reduction of drag	Webb (1984)
Aspect ratio of the caudal fin	$\frac{CFd^2}{CFs}$	CFar	Caudal fin use for propulsion and/or direction	Webb (1984)
Fins surface ratio	$\frac{2 * PFs}{CFs}$	Frt	Main type of propulsion between caudal and pectoral fins	Villéger <i>et al.</i> , 2010
Fins surface to body size ratio	$\frac{(2 * PFs) + CFs}{\frac{\pi}{4} * Bw * Bd}$	Fsf	Acceleration and/or maneuverability efficiency	Villéger <i>et al.</i> , 2010
Body mass	$\log(Massa + 1)$	LogM	Metabolism, endurance, and swimming ability	Villéger <i>et al.</i> , 2010

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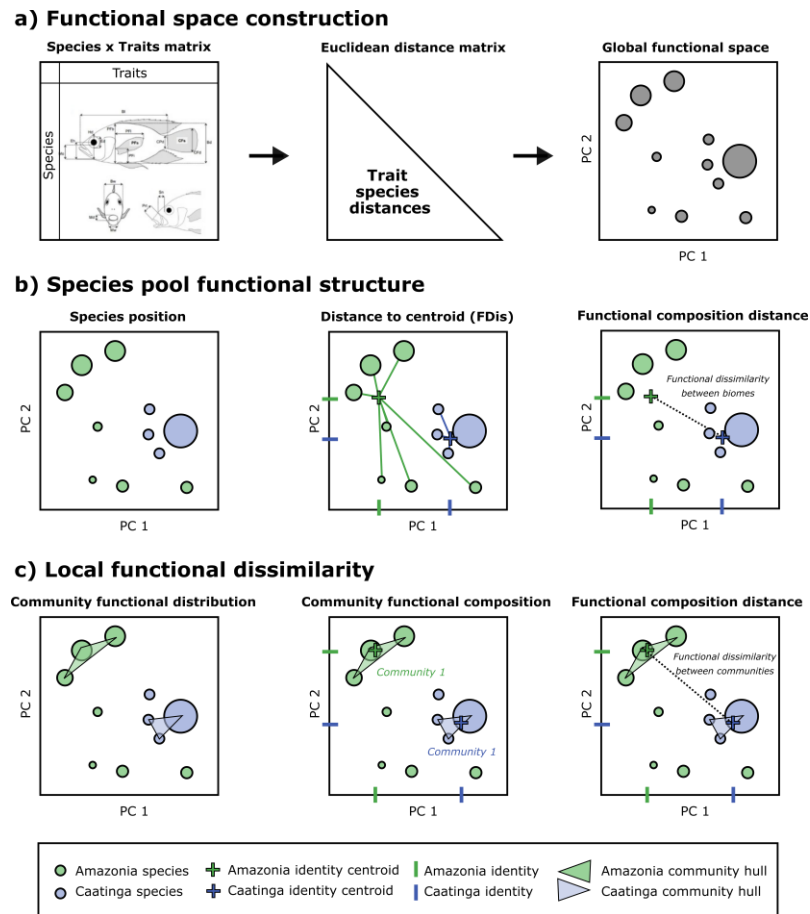


Figure S4.2 Schematic representation of the calculation steps carried to quantify the species pool functional structure and local functional dissimilarity. (a) trait functional space is created by calculating the Euclidean distance between all pairs of species and then applying Principal Component Coordinates Analysis (PCA) resulting in a global functional space that includes both Amazonia and Caatinga species. (b) the differences in the functional structure between the two regional species pools are based on the distance between the centroids (SPF $\beta$ ) and the ratio between species pool functional diversity (SPFDdiff). SPF $\beta$  for each biome is expressed as the mean distance of each species to the centroid of the respective biome. (c) local functional dissimilarity is based on the distance between community centroids. Two PC axes were represented in the scheme to facilitate visualization but note that all functional indexes were calculated from the first four PC axes (see main text).

Table S2.2 Functional trait loadings explained variance and biological interpretation of each Principal Component axes (PC). Correlations > 0.5 are shown in bold.

Functional traits	Abbreviations	PC1	PC2	PC3	PC4
Mass	LogM	-0.260	0.205	<b>-0.590</b>	<b>-0.509</b>
Oral-gape surface	Osf	0.016	0.140	-0.198	-0.077
Oral-gape shape	Osh	0.664	0.123	-0.175	-0.115
Oral-gape position	Ops	0.340	0.577	-0.315	0.315
Mouth-protrusion length	Prt	-0.185	-0.082	<b>-0.671</b>	0.468
Eye size	Edst	<b>0.774</b>	-0.043	0.120	0.282
Eye position	Eps	<b>-0.760</b>	-0.262	0.034	-0.217
Body transversal shape	Bsh	0.503	0.486	-0.379	0.034

Body transversal surface	Bsf	0.169	-0.259	<b>0.547</b>	<b>0.551</b>
Pectoral-fin position	PFps	-0.514	-0.003	-0.410	<b>0.536</b>
Aspect ratio of the pectoral fin	FPar	<b>0.788</b>	-0.016	0.234	0.113
Caudal-peduncle throttling	Cpt	0.516	<b>-0.638</b>	-0.126	-0.325
Aspect ratio of the caudal fin	Cfar	<b>0.747</b>	-0.282	-0.194	-0.356
Fins surface ratio	Frt	0.050	<b>-0.779</b>	-0.374	-0.040
Fins surface to body size ratio	Fsf	0.132	<b>-0.732</b>	-0.276	0.366
Explained variance		25.6%	16.1%	12.8%	11.3%

### Supporting information 3: R scripts

To investigate the effect of the difference in species pool functional structure between regions (SPFD<sub>diff</sub> and SPF $\beta$ ), we resampled 10 local assemblages (1,000 times) for each biome (Amazonia and Caatinga). We follow four specific rules (see main text) to ensure that our resamples are composed by a subset of streams with similar spatial extent and are located at the same hydrological basins. Furthermore, our code provides malleable options to define the similarity of streams between resamples. Initially, we built a function to quantify the spatial extent of the sample's sites within each biome. We provide two different criteria, which are based on maximum distance among sites (called "max") and the polygon convex hull (called "area"). In this study, we used only the argument "area".

The balanced resampling analysis was implemented using a combination of two functions: `spatial_extent` and `balanced_resamp`.

The `spatial_extent` works with the following arguments:

- `coord`: matrix with geographical coordinates in decimal degrees, with longitude and latitude information.
- `biome`: vector object with the biome identity – Amazonia or Caatinga
- `e`: spatial extent criteria. "area" for the area of the minimum polygon convex and "max" for the maximum distance among streams.

**R code:**

```

spatial_extent <- function(coord,biome,e){

#Loading required packages

require(spatstat)
require(adehabitatHR)

#Empty vector

spatial_extent <- numeric(length(levels(region)))

#Maximum distance among sites

if(e=="max"){
for(i in 1:length(levels(region))){
  spatial_extent[i] <-max(dist(coord[which(region ==levels(region)[i]),]))}
}

#Area of the minimum polygon convex

if(e=="area"){
for(i in 1:length(levels(region))){spatial_extent[i] <-
(mcp(SpatialPoints(coord[which(region==levels(region)[i]),]),unin="km",unout="km2",
percent=100)$area) }
}

#From degrees to km/km2

spatial_extent <- data.frame(spatial_extent*111.111)
colnames(spatial_extent) <- "Espatial_extent"
rownames(spatial_extent) <- c(levels(region)[1],levels(region)[2])

return(spatial_extent)

##End of the function spatial_extent

```

The `balanced_resamp` works with the following arguments:

- `coord`: matrix with geographical coordinates of all samples (107 streams) in decimal degrees, with longitude and latitude information.
- `biome`: vector object with the biome identity – Amazonia or Caatinga.
- `basin`: vector object with the basin identity within each biome.
- `Nsite`: number of desired local assemblages in each biome.
- `Nresamp`: number of total resampling. This argument is responsible to generate a high amount of resamples to posterior selection following the specific rules (see above).
- `N`: number of desired resamples.

- `spatial.criteria`: the extent criteria employed. “area” for the area of the minimum polygon convex and “max” for the maximum distance among streams.
- `spatial.threshold`: a threshold above which the geographical extent of streams within each biome is considered small enough to be included. For example, if `spatial.threshold = 250`, the function will exclude the resamples in which at least one of the biomes the spatial extent are greater than 250 km/km<sup>2</sup>. The unit depends on the argument `spatial.criteria`.
- `site.threshold`: a threshold above which the streams composition within each biome is considered too similar. For example, if `site.threshold = 0.7` the function will exclude the resamples that share more than 70% of stream similarity.
- `print.progress`: a logical argument indicating whether the progress of the function `balanced_resamp` must be printed in the screen.

### R code:

```
balanced_resamp <- function(coord, biome, basin, Nsite, Nresamp, N, spatial.criteria=, spatial.threshold,
site.threshold,print.progress){
```

#### #Loading required packages

```
require(dplyr)
require(vegan)
```

#### #Preparing the whole dataset

```
all_data <- data.frame(coord,region,basin)
```

#### #Starts selecting randomly a set of 10 streams in each biome.

#### #All the 10 streams must be located at the same hydrological basin

```
reg1 <- filter(all_data,all_data[,3]==levels(all_data[,3])[1])
reg2 <- filter(all_data,all_data[,3]==levels(all_data[,3])[2])
comb.reg1 <- distinct(reg1[,3:4])[2]
comb.reg2 <- distinct(reg2[,3:4])[2]
```

#### #Randomizing samples between biomes and within each watershed

```
empty.list <- sapply(rep(NA,Nresamp),list)
for(i in 1:Nresamp){
empty.list[[i]] <- c(sample(rownames(filter(reg1,-c(3:4))),
reg1[,4]==as.character(sample(comb.reg1[,1])[1]))) [1:Nsite],
sample(rownames(filter(reg2,-c(3:4))),reg2[,4]==as.character
(sample(comb.reg2[,1])[1]))) [1:Nsite]})
```

#### #After this step we have a list containing 10 riches in each biome, #located inside the same hydrographic basin

```
#-----#
# The following debugs the dataset resampling #
# to ensure specific conditions within and #
```

```

# between biomes #
#-----#

#1. Starts calculating the spatial extent of resampled dataset #Exclude the resampling with spatial extent more than #"spatial.threshold"

which.sel <- numeric()
for(i in 1:Nresamp){
  scale.calc <- spatial_extent(all_data[empty.list[[i]],1:2],
all_data[empty.list[[i]],3],e=spatial.criteria)[c(1,2),]
  boolean.scale <- scale.calc[1] < spatial.threshold & scale.calc[2] < spatial.threshold
  if(boolean.scale == T){which.sel[i]=1}
  if(boolean.scale == F){which.sel[i]=0}
}

#List of resampling with spatial extent less than the #spatial.threshold

L.sel <- list()
count=1
for(i in 1:Nresamp){
  if(which.sel[i]==1)
    count=count+1
  L.sel[[count]] <- all_data[empty.list[[i]],]
}

#2. Removing resampling's with high similarity of stream composition. #This step ensures that resampling's can be considered as independent #at a threshold of 70%

L.diss <- list()
count=1

for(i in 1:length(L.sel)){
if(print.progress==TRUE) message('Select dataset with less than site.threshold criteria - ', i, ' of ',
length(L.sel))
flush.console()

  cand.resamp <- L.sel[[i]]
  if(sum(unlist(lapply(L.sel,function(x)
nrow(intersect(cand.resamp,x))/
nrow(union(cand.resamp,x)) >site.threshold)))==1)
  {
    L.diss[[count]] <- all_data[rownames(L.sel[[i]]),]
    count=count+1
  }
}

##3. Ensuring that all river basins are well represented

basins_res <- list()
for(i in 1:length(L.diss)){
  basins_res[[i]] <- paste(L.diss[[i]][1,4], L.diss[[i]][Nsite+1,4],sep="_")
}

#Defines the desired number of comparisons between basins

```

```

identity_comp <- names(table(unlist(basins_res)))
number_comp <- length(identity_comp)
desired_N <- N/number_comp

chosen_res <- list()
for(i in 1:length(identity_comp)){
  chosen_res[[i]] <- sample(which(basins_res==identity_comp[i])) [1:desired_N]
}

##4. Creating the output of the resamples

output <- L.diss[unlist(chosen_res)]
return(output)

}#End of the function balanced_resamp

```

#### Supporting information 4: Species pool definition based on locally absent species

A reference species pool includes all species that may potentially colonize a specific site (Pärtel et al. 2012). In practice, the species pool is often the list of species in the dataset. For example, the species pool of a set of 10 sites could be estimated by the simple sum of captured species in those streams. The species pool can be defined by considering the locally absent species. Following the formal definition, for a given species to be part of the species pool it must be able to reach and inhabit the local communities. In this study, the estimation of the species pool based on absent species considers that the probability that a species can disperse to a given community must be high. Thus, the species pool based on absent species is site specific making possible that different set of communities within the same region have different species pool (Pärtel et al., 2013). For this, we determinate the species able to disperse to local community using species co-occurrence pattern, using *beals* function (vegan package, Okasanen et al. 2013) to perform co-occurrence probability calculations. According to Beals index, species that usually co-occur can be treated as indicators for the presence of species that occur under the same local environmental conditions in each assemblage (Brown et al., 2019). A species was included in the species pool if its occurrence probability was greater than 5% of occurrence probability in sites where the specie was present.

#### References

- Brown, J. J., Mennicken, S., Massante, J. C., Dijoux, S., Telea, A., Benedek, A. M., Götzenberger, L., Májeková, M., Lepš, J., Šmilauer, P., Hřček, J., & de Bello, F. (2019). A novel method to predict dark diversity using unconstrained ordination analysis. *Journal of Vegetation Science*, 30(4), 610–619. <https://doi.org/10.1111/jvs.12757>
- Pärtel, M., Szava-Kovats, R., & Zobel, M. (2013). Community Completeness: Linking Local and Dark Diversity within the Species Pool Concept. *Folia Geobotanica*, 48(3), 307–317. <https://doi.org/10.1007/s12224-013-9169-x>



Table S5.1. Observed and estimated ( $\pm$ SE) species richness according to four incidence-based estimates (Chao, Jackknife of first order, Jackknife of second order and bootstrap) for Amazonia and Caatinga stream fish.

Biome	Observed	chao	jack1	jack2	boot
Amazonia	140	205.1 ( $\pm$ 5.93)	186.0 ( $\pm$ 2.00)	217 ( $\pm$ 3.52)	158 ( $\pm$ 1.37)
Caatinga	46	52.5 ( $\pm$ 1.59)	56.7 ( $\pm$ 0.87)	58.8 ( $\pm$ 2.02)	51.4 ( $\pm$ 0.55)

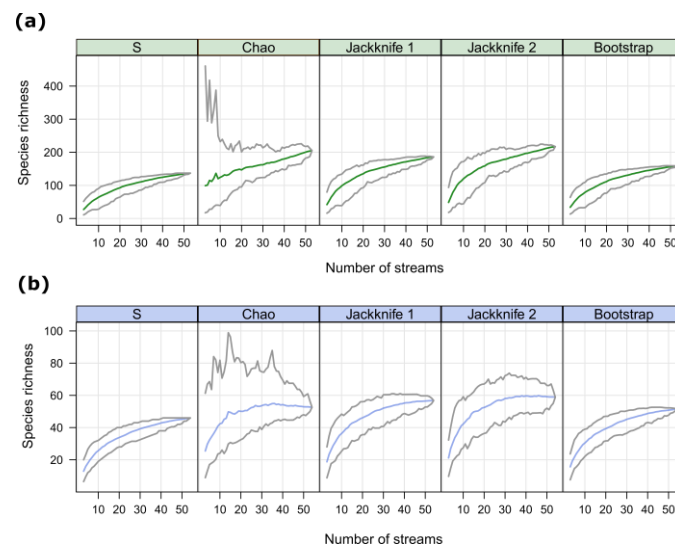


Figure S5.1 Observed and estimated species accumulation curves for the incidence-based estimates for Amazonia (a) and Caatinga (b). Gray lines are 95% confidence intervals.

## Supporting information 6: Resampling results

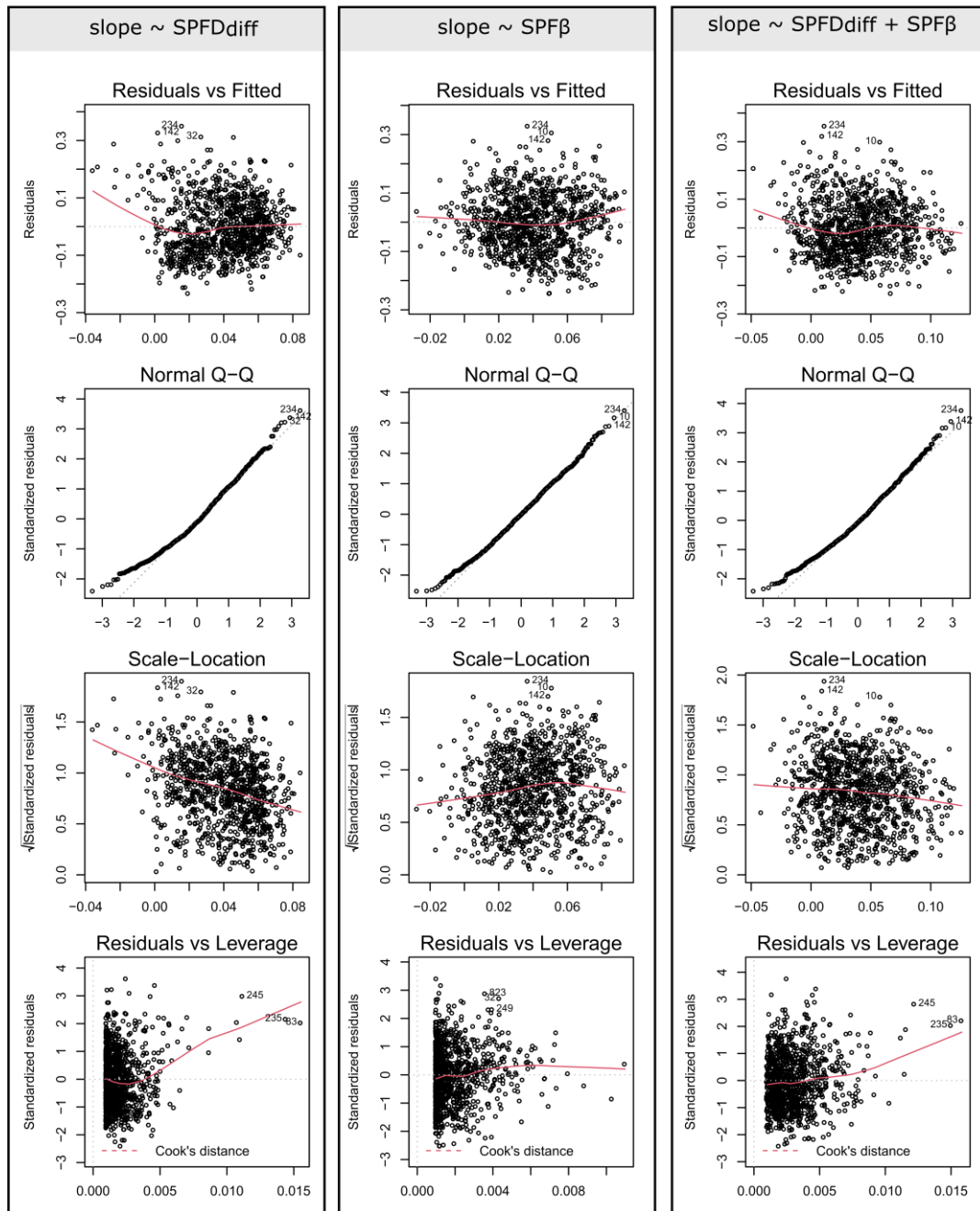


Figure S6.1 Plots to assess model quality and assumptions for the linear regressions between functional composition-environment relationships ( $r$  slopes) and difference in species pool functional structure ( $SPFD_{diff}$  and  $SPF\beta$ ) between regions. Residuals vs Fitted values and Scale-Location are plot for test heteroscedasticity, QQ-plot for normality, and standardized residuals versus leverage, and the Cook statistic for outliers of exploratory variables. The species pool was estimated based on locally present species.

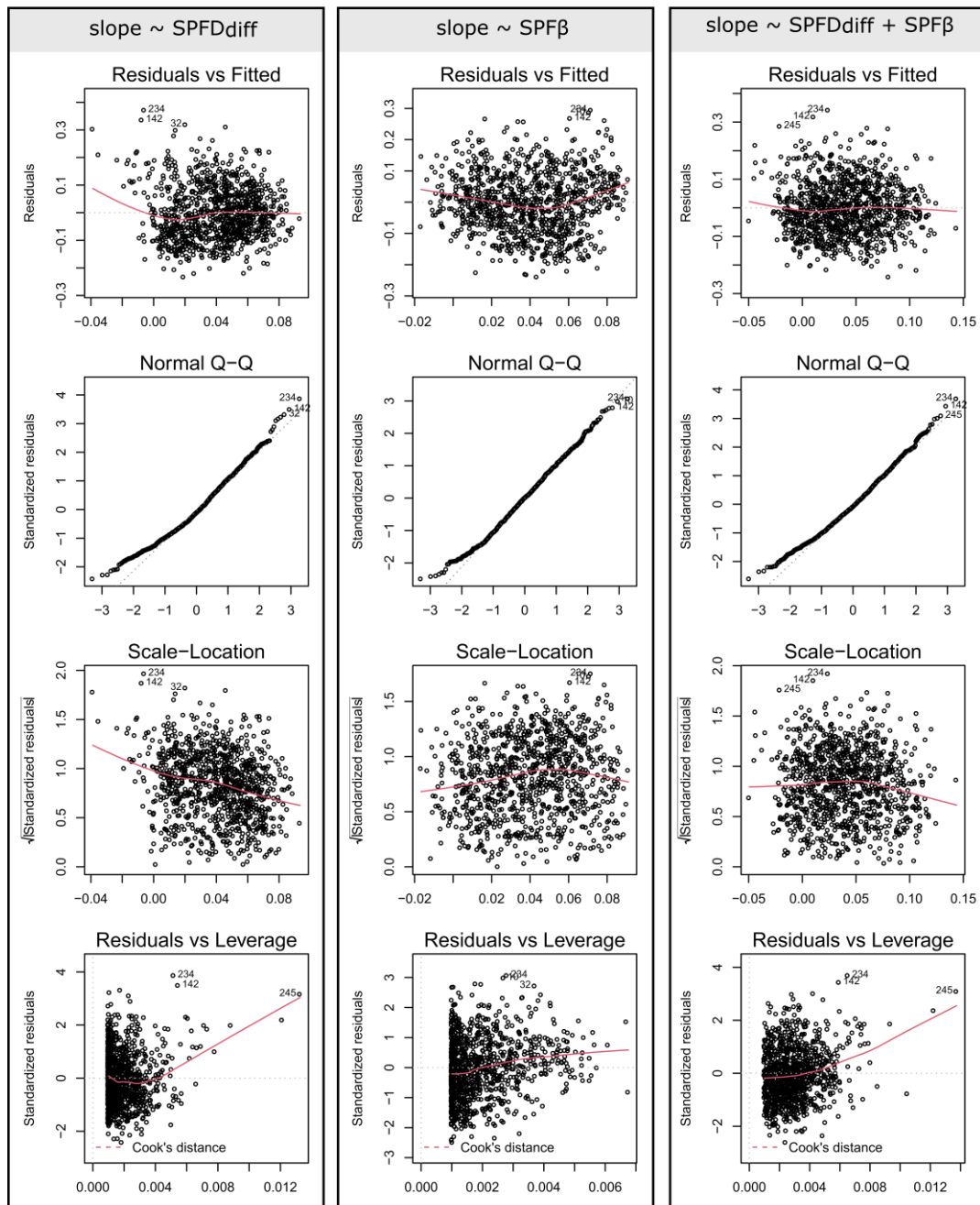


Figure S6.2 Plots to assess model quality and assumptions for the linear regressions between functional composition-environment relationships ( $r$  slopes) and species pool functional structure (SPFD<sub>diff</sub> and SPF $\beta$ ) between regions. Residuals vs Fitted values and Scale-Location are plot for test heteroscedasticity, QQ-plot for normality, and standardized residuals versus leverage, and the Cook statistic for outliers of exploratory variables. The species pool was estimated based on locally absent species (see Supporting information 4).

Table S6.1 Hierarchical models used to determine under which conditions  $SPFD_{diff}$ ,  $SPF\beta$ , are most likely to explain the relationship between environmental and functional dissimilarity among stream fishes of Amazonia and Caatinga (r slopes) using the species pool based on locally absent species. The best ranked model is shown in bold. (\*) represents significantly slopes in comparison with the null model.

Models	Intercept	$\beta$ Parameter		Akaike information		
		$SPFD_{diff}$	$SPF\beta$	AICc	$\Delta AICc$	$\omega AICc$
<b>slope ~ <math>SPFD_{diff}</math> + <math>SPF\beta</math></b>	<b>0.28</b>	<b>-0.01</b>	<b>-0.06*</b>	<b>-1906.4</b>	<b>0.00</b>	<b>1.00</b>
slope ~ $SPF\beta$	0.11		-0.05*	-1840.4	65.97	0.00
slope ~ $SPFD_{diff}$	0.19	-0.01		-1834.8	71.57	0.00
slope ~ Intercept	0.04			-1783.7	122.70	0.00

**Supporting information 7: Species list**

Table S7.1 List of species captured in Amazonia and Caatinga streams.

Order	Family	Species	Code	Biome		
				Amazonia	Caatinga	
Characiformes	Acestrorhynchidae	<i>Acestrorhynchus falcatus</i>	ace.falc	X		
	Anostomidae	<i>Leporinus piau</i>	lep.piau		X	
		<i>Leporinus taeniatus</i>	lep.taen		X	
	Aphyocharacinae	<i>Axelrodia stigmatias</i>	axe.stig	X		
	Characidiinae	<i>Ammocryptocharax elegans</i>	amm.eleg	X		
		<i>Ammocryptocharax minutus</i>	amm.minu	X		
		<i>Characidium bimaculatum</i>	cha.bima		X	
		<i>Elachocharax junki</i>	ela.junk	X		
		<i>Elachocharax mitopterus</i>	ela.mito	X		
		<i>Elachocharax pulcher</i>	ela.pulc	X		
		<i>Melanocharacidium dispilomma</i>	mel.disp	X		
		<i>Melanocharacidium pectorale</i>	mel.pect	X		
		<i>Microcharacidium eleotrioides</i>	mic.eleo	X		
		<i>Microcharacidium weitzmani</i>	mic.weit	X		
		<i>Odontocharacidium aphanes</i>	odo.apha	X		
		Characinae	<i>Charax condei</i>	cha.cond	X	
			<i>Charax macrolepis</i>	cha.macr	X	
			<i>Phenacogaster calverti</i>	phe.calv		X
	<i>Phenacogaster retropinnus</i>		phe.retr	X		
	Cheirodontinae	<i>Priocharax ariel</i>	pri.arie	X		
		<i>Compsura heterura</i>	com.hete		X	
		<i>Serrapinnus heterodon</i>	ser.hete		X	
	Crenuchinae	<i>Serrapinnus piaba</i>	ser.piab		X	
		<i>Crenuchus spilurus</i>	cre.spil	X		
	Curimatidae	<i>Steindachnerina notonota</i>	ste.noto		X	
	Erythrinidae	<i>Erythrinus erythrinus</i>	ery.eryt	X		
		<i>Hoplias curupira</i>	hop.curu	X		
<i>Hoplias malabaricus</i>		hop.mala	X	X		
<i>Hoplerythrinus unitaeniatus</i>		hop.unit	X			
Gasteropelecidae	<i>Carnegiella marthae</i>	car.mart	X			

	<i>Carnegiella strigata</i>	car.strig	X	
Heterocharacinae	<i>Gnathocharax steindachneri</i>	gna.stei	X	
	<i>Heterocharax virgulatus</i>	het.virg	X	
Iguanodectidae	<i>Bryconops caudomaculatus</i>	bry.caud	X	
	<i>Bryconops giacopinii</i>	bry.giac	X	
	<i>Bryconops inpai</i>	bry.inpa	X	
	<i>Iguanodectes geisleri</i>	igu.geis	X	
	<i>Iguanodectes purusii</i>	igu.pru	X	
	<i>Iguanodectes variatus</i>	igu.vari	X	
Prochilodontidae	<i>Prochilodus brevis</i>	pro.brev		X
Pyrrhulininae	<i>Copella nattereri</i>	cop.natt	X	
	<i>Copella nigrofasciata</i>	cop.nigr	X	
	<i>Copella</i> sp. pyrr.	cop.sp.pyrr	X	
	<i>Nannostomus digrammus</i>	nan.digr	X	
	<i>Nannostomus eques</i>	nan.eque	X	
	<i>Nannostomus marginatus</i>	nan.marg	X	
	<i>Nannostomus trifasciatus</i>	nan.trif	X	
	<i>Pyrrhulina aff brevis</i>	pyr.aff.brev	X	
	<i>Pyrrhulina zigzag</i>	pyr.zigz	X	
Serrasalminae	<i>Serrasalmus rhombeus</i>	ser.rhom		X
Spintherobolinae	<i>Amazonspinther dalmata</i>	ama.dalm	X	
Stethaprioninae	<i>Astyanax bimaculatus</i>	ast.bima		X
	<i>Astyanax fasciatus</i>	ast.fasc		X
	<i>Astyanax maculisquamis</i>	ast.macu	X	
	<i>Astyanax</i> sp.	ast.sp		X
	<i>Astyanax</i> sp. balbina	ast.sp.bal	X	
	<i>Ctenobrycon spilurus</i>	cte.spil		X
	<i>Hemigrammus analis</i>	hem.anal	X	
	<i>Hemigrammus bellottii</i>	hem.bell	X	
	<i>Hemigrammus</i> cf. pretoensis	hem.cf.pret	X	
	<i>Hemigrammus coeruleus</i>	hem.coer	X	
	<i>Hemigrammus iota</i>	hem.iota	X	
	<i>Hemigrammus jaguaribensis</i>	hem.jagu		X
	<i>Hemigrammus melanochrous</i>	hem.mela	X	
	<i>Hemigrammus ocellifer</i>	hem.ocel	X	
	<i>Hemigrammus rodwayi</i>	hem.rodw		X

		<i>Hemigrammus schmardae</i>	hem.schm	X	
		<i>Hemigrammus</i> sp. <i>geisleri</i>	hem.sp.geis	X	
		<i>Hemigrammus stictus</i>	hem.stic	X	
		<i>Hemigrammus vorderwinkleri</i>	hem.vord	X	
		<i>Hyphessobrycon</i> cf. <i>agulha</i>	hyp.cf.agul	X	
		<i>Hyphessobrycon heterorhabdus</i>	hyp.hete	X	
		<i>Hyphessobrycon melazonatus</i>	hyp.mela	X	
		<i>Hyphessobrycon parvellus</i>	hyp.parv		X
		<i>Jupiaba zonata</i>	jup.zona	X	
		<i>Moenkhausia collettii</i>	moe.coll	X	
		<i>Moenkhausia comma</i>	moe.comm	X	
		<i>Moenkhausia cotinho</i>	moe.coti	X	
		<i>Moenkhausia dichrourea</i>	moe.dich		X
		<i>Moenkhausia hemigrammoides</i>	moe.hemi	X	
		<i>Moenkhausia lepidura</i>	moe.lepi		X
		<i>Moenkhausia oligolepis</i>	moe.olig	X	
		<i>Moenkhausia</i> sp. <i>lepidura curta</i>	moe.sp.lepcu	X	
		<i>Thayeria</i> cf. <i>obliqua</i>	tha.cf.obli	X	
	Stevardiinae	<i>Tytocharax madeirae</i>	tyt.made	X	
	Tetragonopterinae	<i>Tetragonopterus argenteus</i>	tet.arge		X
		<i>Tetragonopterus</i> sp.	tet.sp	X	
		<i>Triportheus signatus</i>	tri.sign		X
Cichliformes	Cichlasomatinae	<i>Acaronia nassa</i>	aca.nass	X	
		<i>Aequidens epae</i>	aeq.epae	X	
		<i>Aequidens pallidus</i>	aeq.pall	X	
		<i>Aequidens</i> sp. <i>mancha ubocular</i>	aeq.sp.mso	X	
		<i>Amatitlania nigrofasciata</i>	ama.nigr		X
		<i>Cichlasoma orientale</i>	cic.orie		X
		<i>Hypselecara coryphaenoides</i>	hyp.cory	X	
		<i>Mesonauta festivus</i>	mes.fest	X	
	Cichlinae	<i>Cichla monoculus</i>	cic.mono		X
		<i>Crenicichla aff menezesi</i>	cre.aff.mene	X	
		<i>Crenicichla menezesi</i>	cre.mene		X
		<i>Crenicichla inpa</i>	cre.inpa	X	
		<i>Crenicichla regani</i>	cre.rega	X	
		<i>Crenicichla</i> sp.	cre.sp	X	



	Geophaginae	<i>Apistogramma agassizii</i>	api.agas	X	
		<i>Apistogramma cf. erythrura</i>	api.cf.eryt	X	
		<i>Apistogramma hippolytae</i>	api.hipp	X	
		<i>Apistogramma steindachneri</i>	api.stei	X	
		<i>Apistogramma taeniata</i>	api.taen	X	
		<i>Crenicara punctulatum</i>	cre.punc	X	
	Polycentridae	<i>Monocirrhus polyacanthus</i>	mon.poly	X	
	Pseudocrenilabrinae	<i>Oreochromis niloticus</i>	ore.nilo		X
		<i>Tilapia rendalli</i>	til.rend		X
Cyprinodontiformes	Poeciliinae	<i>Poecilia reticulata</i>	poe.reti		X
		<i>Poecilia vivipara</i>	poe.vivi		X
		<i>Xiphophorus hellerii</i>	xip.hell		X
	Rivulinae	<i>Anablepsoides cf. urophthalmus</i>	riv.cf.urop	X	
		<i>Anablepsoides sp. bandas na cauda</i>	riv.sp.bcau	X	
		<i>Anablepsoides micropus</i>	riv.micr	X	
		<i>Laimosemion dibaphus</i>	riv.diba	X	
		<i>Laimosemion kirovskyi</i>	riv.kiro	X	
		<i>Anablepsoides aff. micropus</i>	riv.aff.micr	X	
Gobiiiformes	Eleotrinae	<i>Microphilypnus ternetzi</i>	mic.tern	X	
Gymnotiformes	Electrophorinae	<i>Electrophorus electricus</i>	ele.elec	X	
	Gymnotinae	<i>Gymnotus carapo</i>	gym.cara	X	
<i>Gymnotus coatesi</i>		gym.coat	X		
<i>Gymnotus coropinae</i>		gym.coro	X		
<i>Gymnotus pedanopterus</i>		gym.peda	X		
<i>Gymnotus sp. geoma</i>		gym.sp.geom	X		
<i>Gymnotus sp. tigrinus</i>		gym.sp.tigr	X		
Hypopomidae		<i>Brachyhypopomus beebei</i>	bra.beeb	X	
		<i>Brachyhypopomus brevirostris</i>	bra.brev	X	
	<i>Brachyhypopomus sp. regani</i>	bra.sp.rega	X		
	<i>Hypopygus lepturus</i>	hyp.lept	X		
	<i>Microsternarchus bilineatus</i>	mic.bili	X		
	<i>Microsternarchus sp. cauda curta</i>	mic.sp.cc	X		
	<i>Microsternarchus sp. cauda longa olho grande</i>	mic.sp.clog	X		
	<i>Racenisia fimbriipinna</i>	rac.frim	X		
		<i>Steatogenys duidae</i>	ste.duid	X	
	Rhamphichthyidae	<i>Gymnorhamphichthys petiti</i>	gym.peti	X	

Siluriformes	Sternopygidae	<i>Eigenmannia</i> aff. <i>trilineata</i>	eig.aff.tril	X		
		<i>Sternopygus aequilabiatus</i>	ste.aequ	X		
	Astrodoradinae	<i>Physopyxis ananas</i>	phy.anan	X		
	Auchenipterinae	<i>Spinipterus</i> aff. <i>acsi</i>	spi.aff.acsi	X		
		<i>Trachelyopterus galeatus</i>	tra.gale	X	X	
	Callichthyidae	<i>Callichthys callichthys</i>	cal.call	X		
		<i>Megalechis picta</i>	meg.pict	X		
	Centromochlinae	<i>Tatia brunnea</i>	tat.brun	X		
		<i>Tatia gyrina</i>	tat.gyri	X		
	Cetopsinae	<i>Denticetopsis seducta</i>	den.sedu	X		
	Corydoradinae	<i>Aspidoras menezesi</i>	asp.mene		X	
		<i>Aspidoras rochai</i>	asp.roch		X	
		<i>Aspidoras</i> sp.	asp.sp		X	
		<i>Aspidoras spilotus</i>	asp.spil		X	
		<i>Corydoras garbei</i>	cor.garb		X	
	Helogeninae	<i>Helogenes marmoratus</i>	hel.marm	X		
	Heptapteridae	<i>Gladioglanis conquistador</i>	gla.conq	X		
		<i>Gladioglanis</i> sp. n. spart	gla.sp.n.spar	X		
		<i>Imparfinis pristos</i>	imp.pris	X		
		<i>Mastiglanis asopos</i>	mas.asop	X		
		<i>Myoglanis koepckeii</i>	myo.koep	X		
		<i>Nemuroglanis</i> sp. n. zua	nem.sp.n.zua	X		
		<i>Rhamdia quelen</i>	rha.quel	X	X	
		Hypoptopomatinae	<i>Acestridium gymnogaster</i>	ace.gymn	X	
			<i>Otocinclus mura</i>	oto.mura	X	
			<i>Parotocinclus cearensis</i>	par.cear		X
	<i>Parotocinclus haroldoi</i>		par.har		X	
	<i>Parotocinclus</i> sp.		par.sp		X	
	Hypostominae	<i>Parotocinclus spilurus</i>	par.spil		X	
<i>Ancistrus</i> aff. <i>hoplogenyis</i>		anc.aff.hopl	X			
<i>Ancistrus dubius</i>		anc.dubi	X			
<i>Ancistrus</i> sp. bolas brancas		anc.sp.bb	X			
<i>Hypostomus jaguribensis</i>		hyp.jagu		X		
Loricariinae	<i>Hypostomus</i> sp.	hyp.sp		X		
	<i>Loricariichthys derbyi</i>	lor.derb		X		
	<i>Rineloricaria</i> cf. <i>phoxocephala</i>	rin.cf.phox	X			

		<i>Rineloricaria lanceolata</i>	rin.lanc	X	
	Pseudopimelodidae	<i>Batrochoglanis raninus</i>	bat.rani	X	
		<i>Microglanis poecilus</i>	mic.poec	X	
	Trichomycterinae	<i>Ituglanis amazonicus</i>	itu.amaz	X	
Synbranchiformes	Synbranchidae	<i>Synbranchus madeirae</i>	syn.made	X	
		<i>Synbranchus marmoratus</i>	syn.marm	X	X
		<i>Synbranchus</i> sp. pintado	syn.sp.pint	X	
		<i>Synbranchus</i> sp. reticulado	syn.sp.reti	X	

## CONCLUSÕES

Entender como as comunidades biológicas são montadas e identificar quais os principais mecanismos pelos quais diferentes padrões de montagem são observados, representa um dos principais objetivos da Ecologia de comunidades. Enquanto biogeógrafos utilizam processos que atuam ao longo de largas escalas temporais (e.g., eventos históricos) para entender os padrões de distribuição das espécies, enquanto ecólogos assumem que processos atuando em fina escala espacial (e.g., seleção de nicho, interações bióticas) são mais importantes (Vellend, 2016; Leibold e Chase, 2018). Essa dicotomia tem se provado o “calcanhar de Aquiles” da Ecologia de comunidades, pois parte do pressuposto que a montagem de comunidades deve ser governada por um ou outro processo. De fato, esse pensamento vem sendo rebatido desde o século passado por Ricklefs (1984), mas apenas na década passada se observa uma crescente de estudos empíricos que explicitamente testam para a importância conjunta de processos que atuam em moldar os padrões de montagem de comunidades (Bender et al., 2013; Warren *et al.*, 2014; William, 2022). Esse pensamento tem se difundido até mesmo para o campo da ecologia funcional, que assume uma forte relação entre atributos ecológicos das espécies (do inglês *functional traits*) com o meio ambiente em que vivem (Díaz e Cabido, 2001; McGill et al., 2006). Ou seja, a montagem de comunidades sob a óptica da abordagem funcional deve ser primariamente governada por mecanismos que atuam em fina escala espacial (e.g., seleção de nicho). De certa forma, esse pensamento se assemelha àquele que tínhamos no século passado - o “calcanhar de Aquiles” da Ecologia de comunidades. Pode-se contar nos dedos os estudos que abordam uma visão eco-evolucionária para a montagem de comunidades sob uma óptica da abordagem funcional (e.g., Schleuter et al., 2010; Rodrigues-Filho et al., 2018; Su et al., 2022). Curiosamente, tais estudos são ainda mais escassos para ecossistemas de riachos, onde em uma recente análise cienciométrica Teresa et al. (2022) registraram apenas um único estudo, entre 78, que abordam questões eco-evolucionárias em conjunto com a abordagem funcional. Nessa tese, utilizei um conjunto de dados de peixes riachos de dois biomas brasileiros (Amazônia e Caatinga) para entender como processos históricos e ecológicos interagem para explicar os padrões de diversidade funcional dentro e entre regiões. Importantes conclusões podem ser feitas a partir dos principais resultados dos três capítulos desenvolvidos ao longo da tese.

No primeiro capítulo, investigamos como a dinâmica de metacomunidades de peixes de riachos de três montanhas (popularmente conhecidas como *brejos de altitude*) da Caatinga brasileira é governada por fatores da histórica filogenética da região, ambientais e espaciais. Diferente do esperado, a história filogenética em conjunto proximidade espacial foram importantes em explicar os padrões de ocorrência de cinco grupos funcionais, apresentando maior relevância do que fatores ambientais (e.g., velocidade da correnteza e tipos de substrato). Portanto, a utilização de modelos preditivos baseados unicamente em fatores ambientais não é adequada para alcançar um completo entendimento da dinâmica de grupos funcionais para peixes de riachos de cabeceira. Em contrapartida, explorar aspectos relacionados a capacidade de dispersão das espécies e da história filogenética da região são cruciais para uma melhor compreensão da distribuição espacial dos grupos funcionais de peixes.

No segundo capítulo, encontramos que peixes de riachos da Amazônia brasileira apresentam valores de diversidade funcional maiores do que o esperado ao acaso. Essa prevalência de assembleias compostas por espécies funcionalmente complementares indica que interações bióticas (e.g., exclusão competitiva) podem ser mais importantes do que previamente esperado para regiões mega diversas, como é o caso da Amazônia. Em adição encontramos que esse padrão é modulado pela por eventos de extinção passada, promovidos por incursões marinhas de ~5 Mya, e por fatores ambientais, tais como cor da água da sub-bacia (e.g., preta, branca e clara) e condições ambientais dos riachos (e.g., velocidade da correnteza e tipo de substrato). Dessa forma, que a utilização de processos que atuam em diferentes escalas temporal e espacial (e.g., históricos e contemporâneos) é fundamental para entender a distribuição espacial da diversidade funcional em peixes de riachos da Amazônia brasileira.

No terceiro capítulo, confrontamos uma das principais premissas da ecologia funcional: condições ambientais locais similares devem produzir assembleias com estrutura funcional similar, independentemente de processos históricos. Interessante, demonstramos que quando maior a diferença na estrutura funcional do conjunto regional de espécies (do inglês *species pool*), menor a força de condições ambientais locais em produzir assembleias com estrutura funcional similar entre assembleias de peixes de riachos da Amazônia e da Caatinga. Assim, maior cuidado deve ser tomado ao se assumir a hipótese básica de forte relação entre ambiente e estrutura funcional das assembleias ao se realizar estudos entre regiões biogeográficas ou até mesmo dentro da mesma região, mas cobrindo largas extensões espaciais. Também encontramos que a diferença na composição funcional do conjunto regional de espécies (i.e., diversidade  $\beta$  funcional) aponta como o principal componente da estrutura funcional responsável por moldar a força da relação entre ambiente e estrutura funcional das assembleias. Esse resultado nos alerta sobre a necessidade de identificar quais mecanismos são responsáveis por produzir diferenças na composição funcional do conjunto regional de espécies entre regiões para, assim, aumentar nossa capacidade de generalizar como mudanças do habitat devem influenciar a estrutura funcional de comunidades biológicas.

Utilizando diversas abordagens analíticas, buscamos nessa tese entender quais mecanismos explicam os padrões de diversidade funcional de peixes de riachos da Amazônia e Caatinga. Encontramos suporte para a ideia de que ambos os processos históricos e ecológicos desempenham um importante papel em governar a formação da assembleia de peixes de riachos, de acordo com suas características funcionais. A partir desses resultados é possível inferir que processos históricos também podem ser considerados filtros que atuam em larga escala temporal, determinando quais combinações de atributos são disponíveis para a posterior atuação de filtros locais (e.g., tipos de habitat local). Também é importante salientar que todas as conclusões geradas nessa tese são fundamentadas sob atributos funcionais de peixes de riachos relacionados a uso do habitat (e.g. morfológicos, tróficos). Tais atributos são considerados de resposta ao ambiente (Teresa et al., 2021), logo os resultados aqui apresentados não podem ser utilizados para sustentar a formulação de hipóteses relacionadas com atributos de efeito (e.g., serviços ecossistêmicos). Focando em atributos de resposta ao ambiente, alertamos que é preciso ter cautela antes de assumir que padrões similares e congruentes de estrutura funcional devem ser esperados entre comunidades ambientalmente similares, mas com diferentes histórias evolucionárias.

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