INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA

PROGRAMAS DE PÓS-GRADUAÇÃO DO INPA

PROCESSOS HISTÓRICOS OU CONDIÇÕES LOCAIS: O QUE GOVERNA A ESTRUTURA FUNCIONAL DE PEIXES DE RIACHOS NEOTROPICAIS DE DIFERENTES REGIÕES BIOGEOGRÁFICAS?

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Manaus, Amazonas

Março, 2017

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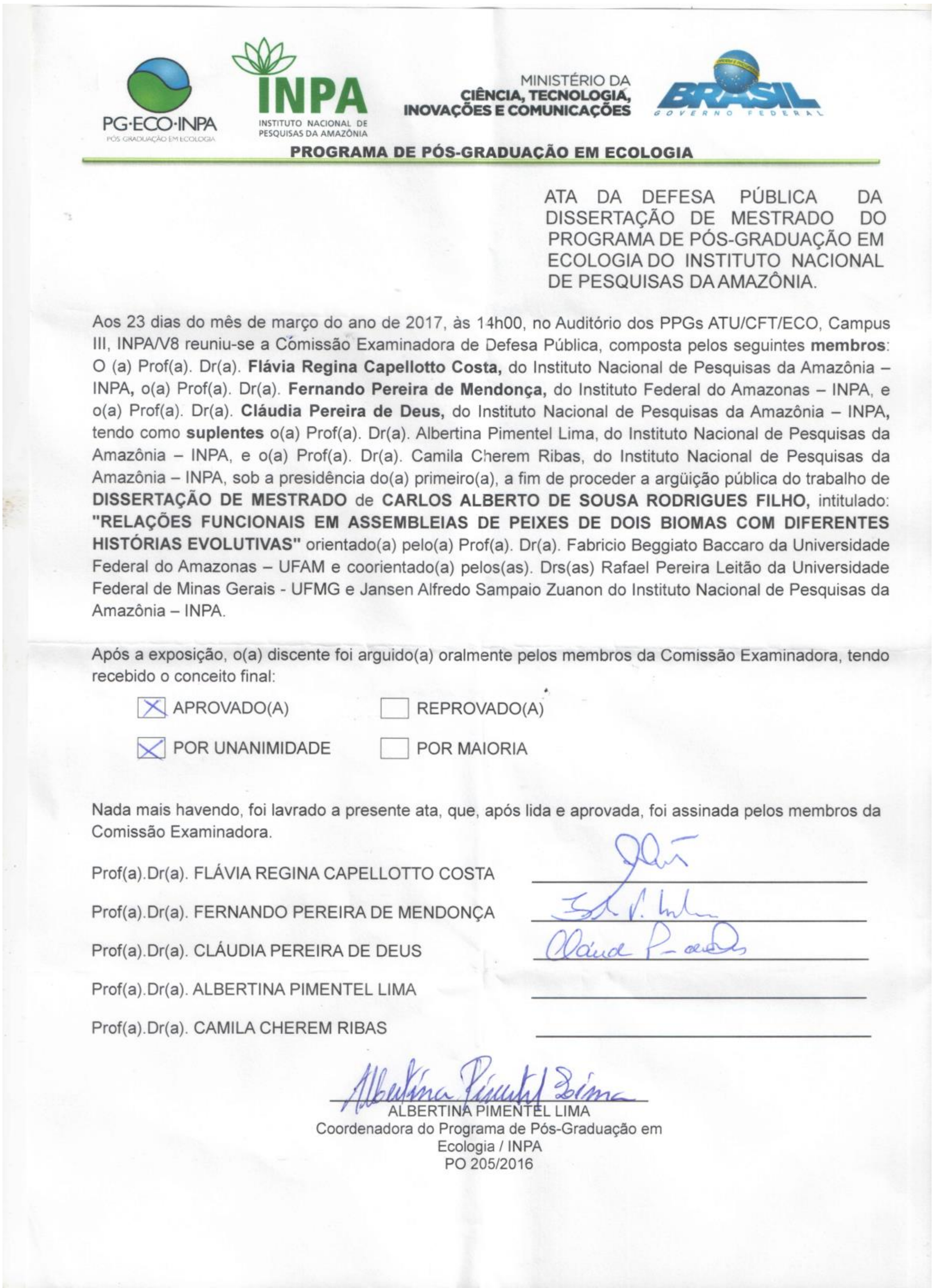
Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte do requerimento para obtenção do título de Mestre em Biologia (Ecologia) em março de 2017.



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Aos 23 dias do mês de março do ano de 2017, às 14h00, no Auditório dos PPGs ATU/CFT/ECO, Campus III, INPA/V8 reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes **membros**: O (a) Prof(a). Dr(a). **Flávia Regina Capellotto Costa,** do Instituto Nacional de Pesquisas da Amazônia – INPA**,** o(a) Prof(a). Dr(a). **Fernando Pereira de Mendonça,** do Instituto Federal do Amazonas – INPA, e o(a) Prof(a). Dr(a). **Cláudia Pereira de Deus,** do Instituto Nacional de Pesquisas da Amazônia – INPA**,** tendo como **suplentes** o(a) Prof(a). Dr(a). Albertina Pimentel Lima, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). Camila Cherem Ribas, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **CARLOS ALBERTO DE SOUSA RODRIGUES FILHO,** intitulado: **"RELAÇÕES FUNCIONAIS EM ASSEMBLEIAS DE PEIXES DE DOIS BIOMAS COM DIFERENTES HISTÓRIAS EVOLUTIVAS"** orientado(a) pelo(a) Prof(a). Dr(a). Fabricio Beggiato Baccaro da Universidade Federal do Amazonas – UFAM e coorientado(a) pelos(as). Drs(as) Rafael Pereira Leitão da Universidade Federal de Minas Gerais - UFMG e Jansen Alfredo Sampaio Zuanon do Instituto Nacional de Pesquisas da Amazônia – INPA.

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

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☒ POR UNANIMIDADE ☐ POR MAIORIA

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PO 205/2016

Ficha catalográfica

R696 Rodrigues Filho, Carlos Alberto de Sousa

Processos históricos ou condições locais: o que governa a estrutura funcional de peixes de riachos neotropicais de diferentes regiões biogeográficas? /Carlos Alberto de Sousa Rodrigues Filho. -- - Manaus: [s.n.], 2017.

90 f.: il.

Dissertação (Mestrado) --- INPA, Manaus, 2017.
Orientador: Fabricio Baccaro
Coorientador: Jansen Zuanon e Rafael Leitão
Área de concentração: Ecologia

1. Diversidade funcional. 2.Peixes de riachos. 3. Perda de espécies. I. Título.

CDD 597

Sinopse

Estudou-se como fatores históricos afetam a estrutura funcional de assembleias de peixes de riachos. Avaliaram-se os níveis de especialização e redundância de funções em biomas que experimentaram diferentes intensidades de distúrbios históricos ao longo de suas histórias evolutivas.

Palavras-Chave: ecologia funcional, distúrbios históricos, peixes de riachos, estabilidade climática.

AGRADECIMENTOS

Esse trabalho contou com o apoio e incentivo de diversas pessoas. Dados utilizados nesse estudo são provenientes do longo e contínuo esforço do grupo de pesquisa do Projeto Igarapés (Coordenado pelo Dr. Jansen Zuanon) e do grupo de pesquisas em peixes de água doce da Universidade Federal do Ceará (Coordenado pelo Dr. Jorge Botero). A todas, meus sinceros agradecimentos.

Muito tenho a agradecer ao Laboratório de Ecologia Aquática (LEA) da Universidade Federal do Ceará (UFC). Foi nesse laboratório onde iniciei minha carreira acadêmica e encontrei o incentivo para prestar a prova de mestrado no INPA. Foi a partir do projeto PPBio de levantamento da Biodiversidade da Caatinga que todos os dados necessários para concluir essa dissertação foram obtidos. Foram cinco anos de muita quilometragem percorrida, mas em muitos casos pouca água encontrada.

Sou imensamente grato aos “homens de ferro” que ao longo de todo esse período me auxiliaram como guias de campo tanto na Caatinga como na Amazônia. Em especial ao seu Fernando que apesar da idade sobe pirambeiras como ninguém e ao Joãozinho e Repolho que me auxiliaram em um dos campos mais difíceis que já participei (Grade do Uatumã). Experiência essa compartilhada com dois amigos que fiz durante o mestrado e que levarei para toda a vida (Lis e Jonas).

Sou extremamente grato ao PPG-Ecologia do INPA pela oportunidade e seus pesquisadores que sempre se mostram de prontidão em nos ajudar nas horas de aperreio. Agradeço a todos os profissionais da secretaria e em especial a Val que faz de tudo para agilizar nossa vida, muito obrigado! Paulinha por sua forma descontraída de nos tratar.

Todas as disciplinas que participei durante esses dois anos me engrandeceram de uma forma ou outra. Agradeço ao Fabricio por ter nos apresentado o programa R e de forma bem descontraída nos mostrou que ele nem é um bicho de sete cabeças (as vezes). Ao Bill por ter revirado nossa mente na sua disciplina de estatística. Flávia por ter apresentado a disciplina de comunidades como nunca tinha visto antes (excelente didática) e por ter me dado a oportunidade de ser monitor no próximo ano. Ao Gonçalo por nos ter feito passar por um “treinamento militar” no KM 41 e nos mostrou o poder de saber manusear o programa R (seus ensinamentos ficaram para a vida). A Juliana por ter me dado apoio logístico durante minha saída de campo e Paulinho por ótimas conversas e trocas de informação sobre biologia funcional. As Dra. Cláudia de Deus e Rafaela Otta por suas

ótimas considerações durante a elaboração deste trabalho. Ao Bill por me proporcionar experiências fora ao mundo do mestrado e por suas sensacionais sacadas sobre nossos resultados. A Albertina por tornar os 15 dias no interior de Novo Airão mais divertidos e produtivos.

Aos pesquisadores Victor Landeiro (UFMT), Fabricio Teresa (UEG), Cecilia Gontijo (UFLA) e Leandro Juen (UFPA) por suas contribuições nas versões iniciais do projeto, ajudando no delineamento.

Em especial aos três pesquisadores que aceitarem me orientar. Ao Fabricio que mesmo sem entender muito sobre peixes encarou de frente o desafio e aposto que agora já consegue debater muito sobre o assunto. Seu interesse e expertise em R me fez querer aprender e me aperfeiçoar sempre mais, fora as longas conversas descontraídas, que sempre me ajudaram nas horas mais complicadas. Ao Jansen (poço de conhecimento) que possui o poder de em apenas 10 minutos nos acalmar, falar sobre a vida e explicar o que cada pontinho do gráfico representa. Ao Rafael Leitão por apresentar imensa paciência nas nossas conversas e me guiar de forma espetacular no mundo da biologia Funcional. A esses três, meus sinceros agradecimentos.

Agradeço a todos da turma de Ecologia de 2015. De certa forma, o conteúdo dessa dissertação contém um pouquinho de todos.

À minha família e namorada que sempre estiveram presentes nas horas mais difíceis da minha vida e do mestrado, sempre me incentivando em todas as ocasiões e tornando esses dois anos longe de casa mais tranquilos.

Ao CNPq pela bolsa de estudos concedida durante os dois anos do mestrado.

“*Somos todos detetives que chegam à cena depois de um crime ter sido cometido*”

Trecho do livro Gene Egoísta de Richard Dawkins.

Resumo

Estudos ecológicos de largas escalas, tem utilizado a abordagem funcional como uma forma de comparar regiões com diferentes composições taxonômicas. Essa abordagem é baseada em características das espécies que afetam direta ou indiretamente seu fitness. Mais recentemente, essa faceta da biodiversidade tem se mostrado muito importante para estudos de conservação, devido a íntima relação entre mudanças ambientais e de diversidade funcional. Nesse contexto, uma das maneiras de entendermos o futuro é compreendendo o passado. Assim, identificar as consequências de fatores históricos e contemporâneos nas assembleias atuais podem nos guiar em futuras tomadas de decisões. Os objetivos desse estudo foram: (i) investigar como a riqueza local de espécies influencia estrutura funcional, (ii) comparar a importância de espécies especialistas e redundantes para cada bioma, utilizando um cenário randômico de perda de espécies, (iii) avaliar a importância de fatores contemporâneos e históricos nos padrões de riqueza e dissimilaridade funcional em peixes de riachos da Amazônia e da Caatinga e (iv) investigar se espécies da mesma ordem apresentam diferentes estratégias funcionais em riachos com condições ambientais semelhantes, mas diferentes histórias de formação. Para isso foi utilizado um banco de dados de assembleias de peixes de 69 riachos dos biomas Amazônia e Caatinga. Como resultado encontramos que fatores históricos apresentam elevada importância para a estrutura local e regional de assembleias de peixes de riachos. Seus efeitos, em combinação com fatores contemporâneos, geram os diversos padrões idiossincráticos observados na literatura, por selecionar diferentes pools de espécies entre regiões. Assembleias que experimentam longos períodos de instabilidade histórica apresentam altos níveis de redundância funcional, possivelmente para suportar as constantes modificações ambientais ao longo do tempo. Resumindo, este estudo reforça a importância de avaliar os fatores históricos em estudos de pequena e larga escala. Contudo, também identificamos ação conjunta de efeitos contemporâneos e históricos, sugerindo que mecanismos complexos e atuando de forma unidirecional (inicialmente filtros históricos seguidos de contemporâneos) são responsáveis por governar os padrões de estrutura funcional em assembleias de peixes de riachos dos biomas Amazônicos e da Caatinga.

Abstract

Functional relations of fish assemblies at two biomes with different evolutionary stories

Ecological studies at large scales have used the functional approach as a way of comparing regions with different taxonomic compositions. This approach is based on species characteristics that directly or indirectly affect your fitness. More recently, this aspect of biodiversity has been very important for conservation studies, due to the close relationship between environmental changes and functional diversity. One way of understanding the future is by understanding the past. Thus, identifying the consequences of historical and contemporary disturbances in the current assemblages can guide us in future decision-making. The objectives of this study were: (i) to investigate how local species richness influences functional structure in each region, (ii) to compare the importance of specialist and redundant species for each biome, using a random scenario of species loss, (iii) to evaluate the importance of contemporary and historical factors in the patterns of richness and functional dissimilarity in the Amazonian and Caatinga streams, and (iv) to investigate whether species of the same order present different functional strategies in streams with similar environmental conditions but different evolutionary history. For this, a database of fish assemblages of 69 streams of the Amazon and Caatinga biomes was used. As a result, we find that historical factors show the great importance of the local and regional structure of stream fish assemblages. In combination with contemporary factors, may be able to generate the various idiosyncratic patterns observed in the literature, by selecting different pools of species between regions. Assemblies experiencing long periods of historical instability have high levels of functional redundancy, possibly to resist the constant environmental changes over time. In summary, this study reinforces the importance of assessing historical factors in small and large-scale studies. However, we have also identified a joint action of contemporary and historical effects, suggesting that complex and unidirectional mechanisms (initially historical filters followed by contemporaries) are responsible for governing the functional structure patterns in stream fish assemblages of Amazonian biomes and the Caatinga.

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Introdução geral

A abordagem funcional tem se mostrado uma importante faceta da biodiversidade, apresentando informações complementares à abordagem taxonômica (Díaz & Cabido, 2001). A diversidade funcional é baseada em características das espécies (traços funcionais) que apresentam link específico com determinados tipos de hábitats (Violle et al. 2007). Por apresentar alta dependência de condições do hábitat (Townsend, 1994), os traços funcionais apresentam maior sensibilidade a mudanças ambientais do que a riqueza taxonômica (Díaz and Cabido, 2001). Por isso inúmeros estudos ecológicos têm utilizado tal abordagem funcional com o objetivo de investigar efeitos de fatores contemporâneas (i.e. condições locais) e históricos (i.e. glaciação, incursões marinhas) (Dobrovolski *et* al., 2012; Leprieur *et al*., 2011) sobre os padrões de diversificação biológica. Outra vantagem da abordagem funcional é comparar assembleias com composições taxonômicas completamente diferentes (Winemiller, 1991; Ernst *et al*., 2012). Nesse contexto, inúmeros estudos realizados em escalas regionais, continentais e intercontinentais utilizam a abordagem funcional para investigar as consequências de eventos passados, como por exemplo diferentes distúrbios entre ecossistemas ou biomas, na estrutura funcional de assembleias (Zimov, 1995; Dobrovolski *et al*., 2012). A universalidade da relação entre as características funcionais das espécies com as condições locais (Poof *et al*., 1997) também tem sido alvo de inúmeros estudos (Ernst *et al*., 2012; Lamouroux *et al*., 2002).

Nesse contexto, desenvolvemos dois capítulos. O primeiro com o objetivo de investigar a importância de eventos históricos em moldar a estrutura funcional de assembleias locais (Capítulo I). O segundo com o objetivo de investigar a importância relativa de fatores contemporâneos e históricos nos padrões de riqueza e dissimilaridade funcional das assembleias (Capítulo II). Tendo em vista os inúmeros registros de padrões idiossincráticos em estudos de larga escala, também investigamos no Capítulo II se espécies da mesma ordem utilizam semelhantes estratégias funcionais entre biomas. A combinação desses resultados com o controle ambiental e a diferença de pool de espécies entre biomas pode nos alertar sobre os mecanismos que promovem padrões idiossincráticos. Para isso utilizamos um banco de dados de 69 riachos (33 na Amazônia e 36 na Caatinga) para atender os pressupostos específicos de cada capítulo.

Objetivos

Objetivo geral

Investigar a importância de fatores contemporâneos e históricos na estrutura funcional de peixes de riachos do bioma da Caatinga e Amazônico.

Objetivos específicos

- Investigar como a riqueza local de espécies influencia estrutura funcional em cada região.
- Comparar a importância de espécies especialistas e redundantes para cada bioma, utilizando um cenário randômico de perda de espécies.
- Avaliar a importância de fatores contemporâneos e históricos nos padrões de riqueza e dissimilaridade funcional em peixes de riachos da Amazônia e da Caatinga.
- Investigar se espécies da mesma ordem apresentam diferentes estratégias funcionais em riachos com condições ambientais semelhantes, mas diferentes histórias de formação.

Capítulo I.

Carlos A. S. Rodrigues-Filho, Rafael P. Leitão, Jansen Zuanon, Jorge I. Sanchéz-Botero and Fabricio B. Baccaro. **Historical disturbance promotes high redundancy and low functional specialization in stream fish assemblages.** Manuscrito submetido – *Functional Ecology*.

Historical disturbances promote high redundancy and low functional specialization in stream fish assemblages

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Summary

1. Disturbances are events that model the structure of biological assemblages, yet few studies have examined how historical disturbances (e.g. marine incursions) can affect the functional structure of recent assemblages.

2. We studied stream fish assemblages from two South American biomes, Amazonia and Caatinga, with different evolutionary histories and levels of environmental stability over time. The high rate of disturbance in the semi-arid Caatinga is known to have promoted environmental instability and biological impoverishment, whereas Amazonia experienced long-term environmental stability. On the other hand, Amazonia was more stable along historical time. We used species functional traits to compare the effects of these historical disturbances in the current structure of stream fish assemblages. For this, we have controlled the effects of current environmental conditions by selecting streams with similar habitats between the two biomes.

3. We used measures of functional similarity to assess the effects of historical disturbances in the structure of fish assemblages. For this, we measured 20 traits in each species, related to locomotion capacity, feeding acquisition and habitat preference. We then computed the functional structure of each assemblage expressed by the functional richness and evenness, and tested the effect of taxonomic richness on these functional metrics. Simulations were subsequently investigated to identify the supposed influence of the loss of specialist species resulting from historical disturbance. If successive losses of species promoted rapid erosion of functional richness, the assemblage would have proportionally more specialist species. On the other hand, if the successive loss of species promoted erosion of functional evenness, the assemblage would show irregularities in the occupation of the functional space. Knowing the evolutionary history of each biome, we should be able to identify how historical disturbance may have affected the functional structure of assemblages.

4. We found high levels of functional specialization in Amazonia and redundancy in Caatinga regional assemblages. These results were also detected in local assemblages, suggesting that the effect of historical disturbance influence the structure of fish assemblages in small and large spatial scales.

5. *Synthesis*. Amazonia showed higher level of functional specialization of the fish fauna in both small and large spatial scales when compared to Caatinga streams, independently of taxonomic richness. The results reinforce the importance of understanding and evaluating the evolutionary history of ecosystems to develop effective conservation strategies of aquatic habitats and its biodiversity.

Key-words Functional structure, Functional biogeography, Stream fish, Historical factors, Species loss, Neotropical freshwaters.

Introduction

Disturbances are important events that modify the structure and diversity of biological communities (Mori 2011). In many cases, they determine the loss of many species (e.g. Ernst, Linsenmair & Roedel 2006), while in others they may constitute key factors allowing species persistence (Pickett & White 1985) or even new establishments (Mori 2011). However, our knowledge about how disturbance operates predominantly comes from studies on short time scales (Ives & Carpenter 2008; Medeiros & Maltchik 2001; Tilman, Reich & Knops 2006). Although highly relevant, such studies have often been criticized by not incorporating measures based on species functional traits and neither evaluating the possible effects of natural historical disturbances (Reiss et al. 2009). Despite this, understanding the importance of natural disturbance in the structure of biological assemblages may help defining better conservation strategies that consider the functional requirements and responses of species assemblages to ongoing global changes (Díaz & Cabido 2001; Buisson et al. 2012; Violle et al. 2014).

One way to understand the effect of future changes in biological systems is studying how past events have influenced biological diversification and the structure of present assemblages (Dobrovolski et al. 2012). Historical events (e.g. tectonic movements, glaciation and marine incursions) are examples of natural disturbances that have shaped the evolutionary history of ecosystems with effects that can be observed in the actual functional structure of assemblages (Gonzalez & Loreau 2009). Some studies investigating the consequences of historical disturbances in present assemblage structure reported that loss of species that play unique functional roles have the pronounced consequences for both assemblage structure and ecosystem functioning (Dobrovolski et al. 2012; Zimov et al. 1995). However, this effect is principally investigated at regional scales and little is known about how historical disturbances shape local assemblages (Tonn 1990) and whether local functional structure are reflective of these events (Ricklefs 2006).

Species that play similar roles are functionally redundant, while complementary species contribute more to the multifunctionality in ecosystems (specialization of functions; Hooper et al. 2005; Mouillot et al. 2011). We can hypothesize how the assemblages' functional structure, represented by functional richness (FRic) and evenness (FEve) measures, respond to the loss of specialization or redundancy promoted by historical disturbances. At low disturbance levels (i.e. environmental stability), competitive interactions tend to promote the co-occurrence of species with dissimilar traits. Conversely, in sites with high disturbance levels (i.e. environmental instability) environmental filters can be more relevant for structuring local assemblages, favoring the co-occurrence of species with similar functional traits (Mouillot, Dumay & Tomasini 2007). Thus, we can predict the effect of historical disturbance in the functional structure of assemblages using simulations of specialist and redundant species loss (Fonseca & Ganade 2001): (1) if assemblages are composed of a high proportion of functionally similar species (i. e. high redundancy), initial losses will promote slower FRic decrease; (2) if the functional space of the assemblage is regularly filled (= abundance equitably distributed) initial losses would not strongly affect FEve, indicating a regular occupation of the functional space. Conversely, assemblages with vacant niches inside the functional space would show a rapid FEve decrease pointing to an irregular occupation of functional space.

The historical events that shaped the hydrography of South America include a long-term natural set of disturbances, which shaped the taxonomic and functional structure of freshwater fish assemblages (Albert & Reis 2011). Tectonic-plate movements, marine intrusions, and climatic change were the main factors affecting the continent over millions of years, isolating or gathering watersheds (Hubert & Renno 2006; Ribeiro 2006). As a result, Amazonian fish assemblages experienced a long time of climatic stability, while the Caatinga fish assemblages experienced various climatic changes and strong environmental disturbances (i.e. climatic changes and marine incursions) (Peres et al. 2010; Santos et al. 2007; Tabarelli & Santos 2004).

Here, we examine the functional structure of two regional assemblages of stream fish that experienced different historical disturbance regimes. For this, we use local and regional analysis to test the effect of historical stability in present patterns of functional structure of fish assemblages. We selected streams of similar topographical conditions (elevation, size, and general environmental conditions) in Amazonia and Caatinga to control for local environmental effects in the observed patterns of functional structure. More precisely, we (i) investigated how the local species richness influence the functional structure of stream fish assemblages in each region, and (ii) compared the importance of specialist and redundant species for each biome, by generating simulations of random species extinction, aiming to better understanding the role of historical disturbances in the functional structure of those stream fish assemblages.

Materials and Methods

Fish sampling and data selection

The analyses were based on inventories of streams in two Brazilian biomes, Caatinga and Amazonia (Fig. S1). Sampling was conducted between 2011 and 2015 (20 stream-sites in each biome) following a standardized sampling protocol (q.v. Mendonça, Magnusson & Zuanon 2005). We select sampling sites from the databases of Projeto Igarapés (http://www.igarapes.bio.br/) and the Laboratório de Ecologia Aquática of the

Universidade Federal do Ceará, searching for streams with similar structural and environmental conditions (for details of the criteria for selecting the streams see Appendix S1, Fig. S1.1).

Nets (3 mm stretched mesh size) blocked each sampling site delimiting a 50-m stretch, and physical and chemical variables were measured. Later, two collectors actively sampled for fish with seines and hand nets during two hours. The collected fishes were euthanized with a lethal concentration of anesthetics (Eugenol), preserved in 10% formalin, and later stored in ethanol 70%. Collecting and euthanizing fishes were conducted under collecting permits from IBAMA and institutional committees for ethics in research with animals. Voucher specimens were deposited at the fish collections of Instituto Nacional de Pesquisas da Amazônia (Manaus, Amazonas state) and Universidade Federal do Rio Grande do Norte (Natal, Rio Grande do Norte state), Brazil.

Environmental conditions, altitudinal gradients and stream order are often considered the main drivers structuring fish assemblages at local scales (Erös et al. 2009; Hoeinghaus, Winemiller & Birnbaum 2007; Mendonça, Magnusson & Zuanon 2005; Poff 1997; Terra, Hughes & Araújo 2015). To characterize the local habitat conditions, channel depth and width, current velocity, canopy cover, temperature, pH, and substrate characteristics were measured. All sampling sites are located at altitudes from zero to 450 m a.s.l. and constitute streams from first to third order. Channel width (m) and depth (m) were measured with a measuring tape and velocity (m/s) was estimated by the time necessary for a styrofoam ball to cover a distance of one meter in the main channel. Water temperature (°C) was registered with a portable Hanna HI9146 device and pH was measured with an electronic probe (PHscan 30). The relative substrate composition (%) were visually classified in eight categories: pebble/gravel (1-

10 mm), sand (0.1-1 mm), clay (0.05-0.1 mm), trunk (> 10 cm), litter, fine litter (organic silt), roots (of riparian vegetation) or macrophytes. The categories pebble/gravel, sand and clay was determined using a ruler.

Functional structure of fish assemblages

Nineteen morphometric measurements (Fig. S2.1) and biomass (g) were taken in adult individuals (n= 3 to 10) of each species to obtain 15 functional attributes related to the locomotion capacity, feeding acquisition and habitat preference. These functional traits are widely used in the literature because they directly affect species fitness (Leitão et al. 2016; Table S2.1).

After standardized and centralized (mean of 0 and standard deviation of 1) the 15 ecomorphological attributes were ordered in a multidimensional functional space using Principal Component Analysis (PCA) using all species pool (Amazonia and Caatinga). We applied the protocol of Maire et al. (2015) to define the number of PCA axes that were retained for subsequent analyses in order to adequately represent the initial functional distance among species. Consequently, the first four axes of PCA (67.9% of accumulated variance explained) were used in the following analyses. From this functional space, the functional structure indices were computed, as described below.

The functional singularity and specialization of each species was respectively measured by the index of Functional Originality (FOri) and Functional Specialization (FSpe). FOri is expressed by the distance between each species and its nearest neighbor in the multidimensional functional space; species tend to be functionally less original (functionally redundant) when they have combinations of traits similar to other species (Mouillot et al. 2013). FSpe is expressed by the Euclidean distance between each species and the centroid of the functional space (Mouillot et al. 2013). Both indexes were standardized between 0 and 1, dividing the value of each species by the respective maximum values of FOri and FSpe measured for the total pool of species.

The functional structure of the assemblages was determined by the indices of Functional Richness (FRic) and Functional Evenness (FEve). FRic is the volume of the convex hull polygon occupied by all species of an assemblage within the functional space (Cornwell, Schwilk, & Ackerly 2006). We standardized FRic values for each assemblage by expressing them as a proportion of the volume filled by the global pool of species. FEve indicates how regularly species abundances are distributed in the functional space, and is constrained between 0 and 1, increasing when species and their abundances are more evenly distributed (Villéger, Mason & Mouillot 2008).

Data analysis

Covariance analyses (ANCOVA) were performed to investigate how local assemblages respond to different levels of historical disturbances. For this, we determine the influence of the local species richness on richness and functional evenness values (FRic and FEve) both within and between biomes. In both models, the taxonomic richness was used as a predictor and the biome as a factor for FRic and FEve separately, with streams as sampling units.

In order to determine how historical disturbances influence the functional structure of assemblages *via* trait diversification (specialization or originality), we created simulation of species loss (q.v. Leitão et al. 2016). We generated two models to evaluate if the loss of more original and more specialized species (higher values of FOri and FSpe) promoted erosion of FRic and FEve greater than expected by chance. The procedure consisted of sequentially removing the species with higher values of FOri and

FSpe, computing the remaining FRic and FEve values. To compare the effect of ordered species loss on the observed values of FRic and FEve we generated a null model by randomly removing species from each assemblage and computing FRic and FEve in each simulation (1,000 times).

Functional diversity indexes were calculated with the functions convhull (FRic, geometry package) and dbFD (FEve, FD package; Laliberté & Legendre 2010). The packages geometry (Habel *et al*. 2014) and cluster (Maechler *et al*. 2016) were used to calculate distances to the nearest neighbor in R software version 3.3.0 (The R Foundation for Statistical Computing).

Results

Ichthyofauna

A total of 109 species were collected in the 40 streams (32 species for the Caatinga and 83 species for the Amazonia, with six species in common to both biomes), distributed in six orders and 15 families. Functional richness (FRic) were higher in the Amazon assemblages, but the regularity (FEve) of occupation of the functional space was similar between biomes (Fig. 1, Fig. S2). Greater values of FSpe and FOri were observed in Amazonia, indicating assemblages composed of more specialized and less original species (Fig. 1).

The Amazonian regional pool is composed of species with FSpe values higher than the Caatinga in most orders (t = 3.13, P = 0.002). Although the species extinction simulation revealed that Caatinga has a greater proportion of original species, the observed FOri values were not significantly lower than those of the Amazonia (t = 1.13, P = 0.114).

Influence of historical disturbance in local assemblages

Richness and functional Evenness differed as a function of the taxonomic richness in the two biomes (Fig. 2). Local species richness explained the variation in FRic within (Richness; P = 0.001) and between (Treatment; P = 0.02) biomes, with Amazonian streams generally presenting greater FRic values than those of Caatinga. On the other hand, there was an interaction between the biome and taxonomic richness (P = 0.02) for FEve, indicating that the relationship between FEve and taxonomic richness is different between biomes. Taken together, these results indicate that occupied volume of the functional space is larger in species-rich places, but in Caatinga assemblages is occupied more regularly.

Impacts of losing functional specialists and original species

The species loss simulations revealed that, for both Amazonia and Caatinga regional assemblages, FRic decreases much faster with few species loss (Fig. 3). This decrease is especially acute in the Amazon. The comparison between the curves of FEve observed values showed that specialization had greater influence in Amazonia, while the redundancy (species originality) was more important in Caatinga. For the Caatinga, FEve values were lower than expected by chance after the loss of the most original species (50% of the loss), while in the Amazon the loss of approximately 55% of the most specialized species resulted in lower FEve than expected by chance. Additional results focusing on the effect of species loss after controlling for taxonomic richness have shown that the patterns observed, except for the impact of losing the most specialists on FEve, are robust even when comparing assemblages with the same number of species (Fig. S3).

Discussion

Taxonomic and functional richness were higher in Amazonia than in Caatinga, at both local and regional scales (Fig. 1, Fig. S3). The functional richness (FRic) decay curves suggest that Caatinga assemblages have greater functional originality (redundancy), whereas those of Amazonia have combinations of unique traits. Given that, losses of few Amazonian species would cause great erosion of functional richness. The analyses of regularity of occupancy of the functional space also suggest that specialization has greater influence in functional evenness in Amazonia, while originality is more important in Caatinga. The same patterns were observed after controlling for the effect of species richness. The selection of environmentally similar streams, combined with the high fidelity of the species to the local habitat (Espírito-Santo et al. 2011), allows us to infer how the historical processes may have shaped the functional structure of the fish faunas in these two biomes.

The different patterns observed for the structure of fish assemblages may have their roots in the historical biogeography of the two regions and their evolutionary trajectories. Along evolutionary time, tropical regions are known to have experienced greater climatic stability than temperate regions, which have promoted high rates of species diversification and lower rates of species extinctions (Gaston & Blackburn 1996). Marine incursions, uprising of the Andes and the formation of geological structural paleoarches were the main events hypothesized to have shaped the ichthyofauna of South America, through limitation of dispersion and extinction of species (Hubert & Renno 2006). The intensity of these events differentially affected certain regions and biomes, such as Amazonia and Caatinga (McCann 2000). After the last glacial period, the Amazon region presented climatic stability (few large-scale disturbances), while the Caatinga experienced other marine incursions, the forested areas were reduced, the regional climate changed (from tropical to semiarid), and extreme dry climatic events occurred (Peres et al. 2010; Tabarelli & Santos 2004). Thus, the higher overall taxonomic and functional richness of Amazonia in relation to the Caatinga is likely to be explained by the environmental stability over the time.

Greater taxonomic richness was accompanied by greater functional richness, suggesting that the functional diversification in the Amazon resulted in increase of species. In fact, less original and more specialized species may be related to evolutionary mechanisms lessening ecological competition for resources (Micheli & Halpern 2005; Mouillot, Dumay & Tomasini 2007). The characteristics of Amazon assemblages indicate that limiting similarity is more important than environmental filters compared to the Caatinga, which is reflected in the levels of specialization and originality of the two assemblages. Similar results can be observed in successional processes of plant assemblies (Lohbeck et al. 2014). Moreover, these results can also be observed on a local scale (biomes), suggesting that the high functional richness of Amazonia results from unique combinations of traits of species that are not found in the Caatinga. Possibly due to the environmental instability of Caatinga that promote more originality in local assemblages (i.e. historical events; Tonn 1990).

It has been well documented that environmental filters acting on regional scales are important for modeling the functional structure of assemblages, even for long periods after disturbances (Hooper et al. 2012; Kulakowski & Veblen 2007). In this study, we can identify two contrasting consequences of disturbances that modelling the ichthyofauna of South America (i.e. marine incursions, climatic changes) in the taxonomic and functional structure of stream fish assemblages. For the Caatinga, the higher environmental instability promotes greater redundancy by decreasing the functional-traits range across species assemblages (Danovaro et al. 2008; Smit et al. 2016).

Environmental instability also increases the risk of biological invasion by eliminating the invasiveness resistance effect promoted by high diversity and functional equitability (Ives & Carpenter 2007). In fact, in Caatinga four introduced (invading) species were recorded, one of which was the third most abundant of all species (*Poecilia reticulata*). On the other hand, environmental stability in the Amazon favored higher values of species richness and ecomorphological variability, contributing to the existence of more specialized niches (Ives & Carpenter 2008). Although we use stream fish assemblages as models for our study, the patterns found may be observed in other taxonomic groups, mainly because the relationship between specialization and originality seems to be universal (Leitão et al. 2016; Mouillot et al. 2011; Micheli & Halpern 2005).

If we consider the Caatinga as a taxonomically and functionally impoverishment subset of the ichthyofauna of the Amazon (Hubert & Renno 2006), we can predict that an intensification of environmental disturbances would promote an initial loss of more specialized species. This prediction has been confirmed in numerous short-term studies that assess the effects of agriculture and introduced species (Flynn et al. 2009; Villéger et al. 2014). In a long-term experiment, Reich et al. (2012) have shown that environmental disturbances lead to functional simplification of assemblages and only a long time, colonization of more specialized species takes place. According to the distribution of the species in the functional space, we can observe that the most specialized ones present lower abundances (black circles of Fig. 1). Possible explanations for low functional specialization in the Caatinga may include higher extinction rates of less abundant species with restricted spatial distribution.

The results found here do not support the main trait-environment selection hypotheses (Poof 1997; Townsend and Hildrew 1994). According to them, the habitat heterogeneity allows the coexistence of species with different competitive abilities that promote the use of a wide range of resources (i.e., space and food). Which was not found in this study, despite the selection of streams with similar environmental conditions between biomes. Thus, the high functional originality and the low species richness in Caatinga streams would be result of biogeographic history and not contemporary conditions (i.e. structure of local habitats). However, it is remarkable that the hypothesis of trait-environment selection does not address how the historical filters influence the functional structure of assemblages, and the results found here can point out to an expansion of such hypothesis. Here we have seen that an important point to be considered in studies that evaluate the functional structure of assemblies of different regions or biomes is their biogeographic histories, which has been shown to be an important driver of changes in assemblages (Cilleros et al. 2016; Ricklefs 2006).

Studies that evaluate the direct effect of species loss on ecosystem functioning are mostly experimental (Díaz et al. 2003). Although they are extremely important to understanding the roles that each species plays in ecosystems, they may result somewhat artificial given the lack of realism. Here we studied two sets of fish assemblages that were separated from each other ~5 million years ago, which gave us the opportunity to investigate what could be considered as a remnant of a natural experiment about the effects of environmental disturbances on the functional dynamics of stream fish assemblages.

Conclusions

We have shown here that historical factors may play a key role in shaping the functional structure of Neotropical stream fish assemblages both at local and regional scales. More specifically, environmental stability favors functional specialization in natural assemblies, while environmental instability promotes high functional originality. Understanding the natural dynamics of each assemblage and its consequences on the local and regional functional structure may be important starting points for delineating appropriate conservation strategies for each case (Cardinale et al., 2008; Mouillot, Dumay & Tomasini 2007; Wallington, Hobbs & Moore 2005). Given the increasing anthropogenic impacts in most ecosystems on Earth (Hooper et al. 2012), these results warn us about how the intensification of disturbances can affect the functional structure of biological assemblages in future.

Acknowledgements

We are grateful to Flávia Costa, Victor Landeiro, Leando Juen, Cecilia Gontijo and Fabricio Teresa for valuable suggestions in early stages of this research. JZ receives a productivity grant from CNPq (#313183/2014-7). The study was funded by CNPq/PPBIO through grant #457463/2012-0 and by CNPq/ICMBio through grant #552009/2011-3. Also thanks to the Ministry of the Environment (MMA; 26174-2) and the Chico Mendes Institute for Biodiversity Conservation (ICMBio/SISBIO; 32921-4) for granting licenses to collect fish samples. This is contribution # XX of the Projeto Igarapés publication series.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Selection of streams with similar environmental conditions and heterogeneity.

Appendix S2 Functional trait assessment.

Fig. S1 Geographic sample location.

Fig. S2 Resume of functional structure of assemblages.

Fig. S3 Simulation of species loss after taxonomic richness control.

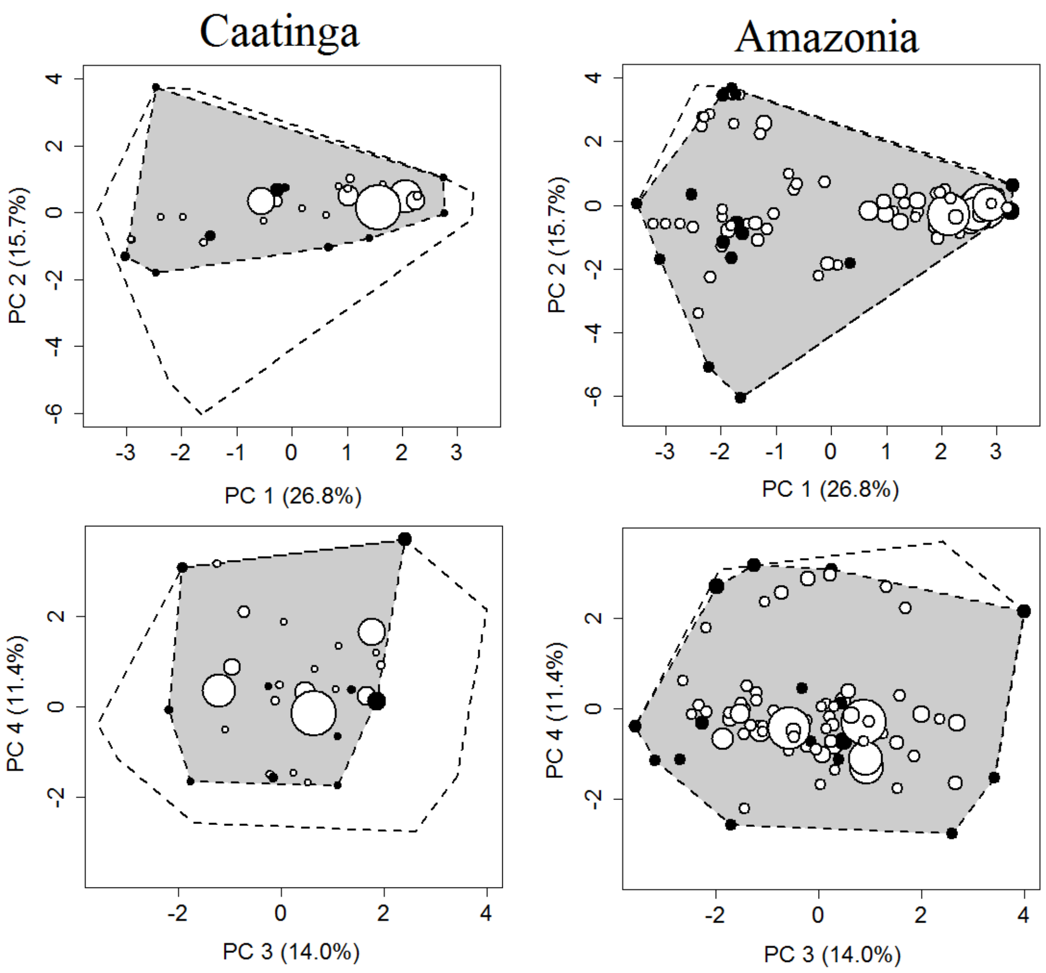

Fig. 1 Multidimensional space on fish ecomorphological traits from regional assemblages of Amazonia and Caatinga. For each assemblage, the first four axes of a Principal Components Analysis (PC) were represented. Black dots correspond to species located on the border of the assemblage functional space within the four axes. The size of the circle is proportional to the relative abundance of the species in each biome. The volume of the functional space occupied by each assemblage is represented by the gray polygon, the dotted line represents the functional space of the entire data set.

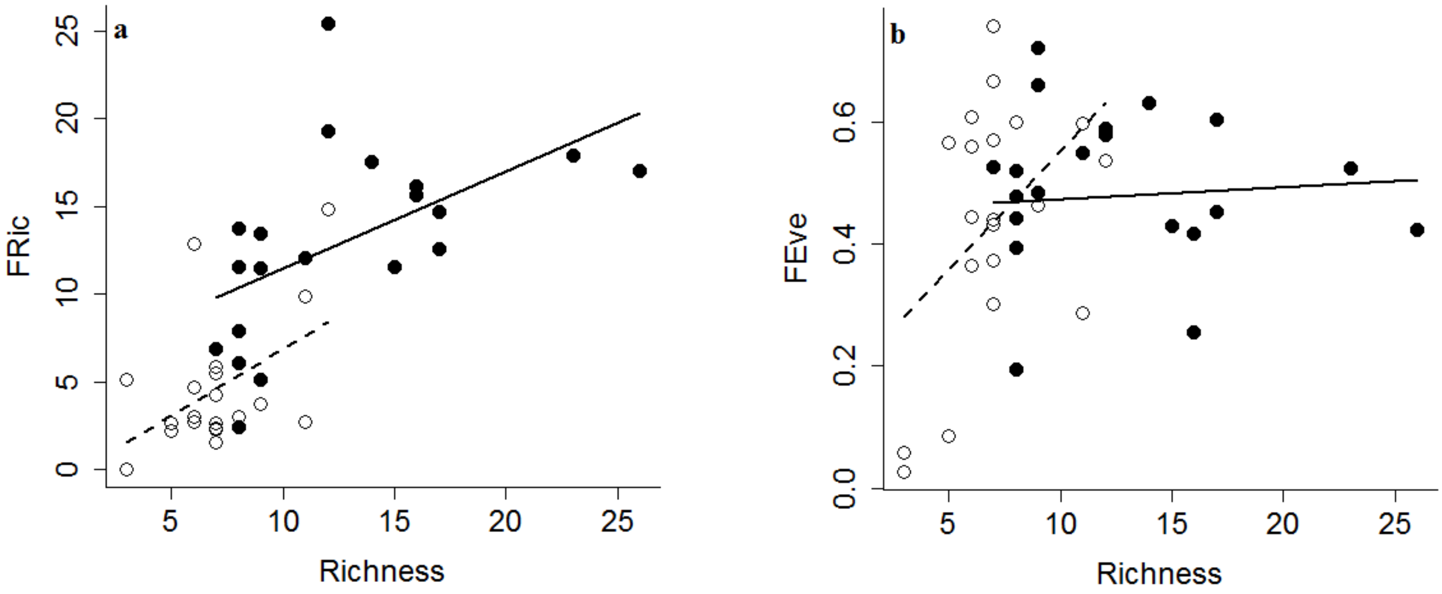

Fig. 2 Linear relationships between species richness and the indices of Functional Richness - FRic (a) and Functional Evenness - FEve (b) for stream fish assemblages from Amazonia (●) and Caatinga (○).

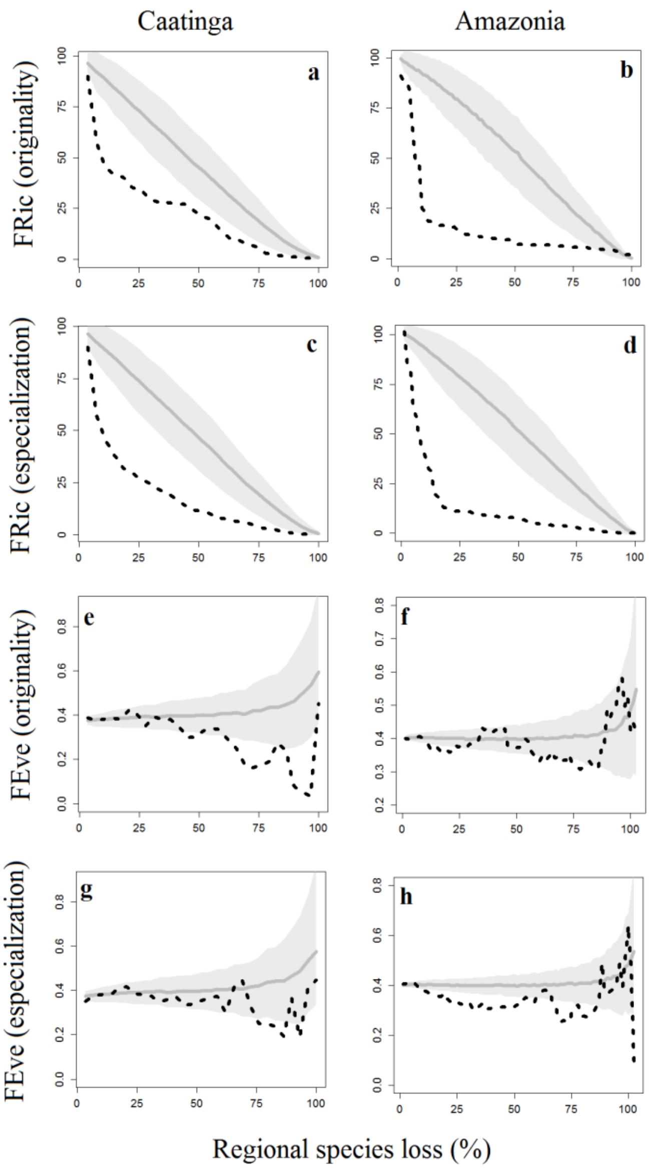

Fig. 3 Impact of losing original and specialist' species on the Functional Richness (FRic) and Functional Evenness (FEve) of regional stream fish assemblages from Amazonia and Caatinga. (a,b,e,f) removing less original first. (c,d,g,h) removing specialist first. Each scenario was contrasted with a random loss of species (gray line and shaded area indicate, respectively, the mean and the 95% confidence interval of the null model).

Capítulo II.

Carlos A. S. Rodrigues-Filho, Rafael P. Leitão, Jansen Zuanon, Jorge I. Sanchéz-Botero and Fabricio B. Baccaro. **Historical and local factors promote idiosyncratic patterns in Neotropical fish assemblages.** Manuscrito em preparação – *Diversity and Distributions*.

ORIGINAL ARTICLE

Historical and local factors promote idiosyncratic patterns in Neotropical fish assemblages

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Running-title: Causes of idiosyncratic patterns in Neotropical fish assemblages

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Key-words Functional uniqueness, Functional dissimilarity, Neotropical freshwater fish, Environmental filters.

ABSTRACT

Aim Assessing the balance between historical and local forces in shape the functional structure of fish assemblages.

Location Amazonian and Caatinga biomes, Brazil, South America.

Methods We selected 52 streams in Caatinga and Amazonia biomes. The selection was based in environmental similarity, so that to promote greater similarity between than within each biome. In resume, 13 streams in each biome present dense canopy cover while 13 do not have canopy cover. Using this scenario, we quantify the richness and functional dissimilarity between assemblages. We also quantify the functional uniqueness of species orders to verify if the occupied niche between assemblies is similar between environments.

Results The functional dissimilarity was greater in assemblages with different environments conditions, independently of biome. In part, the greater functional richness in uncovered streams. However, the occupied niche of species was different between and within biome. This suggests that the species pool selected by historical filters is the response by the observed idiosyncratic patterns and high specialization in fish fauna of South America.

Main conclusions The joint action between historical and local factors promote idiosyncratic patterns and high functional specialization in fish fauna of South America. This result alert us about the importance of investigate the evolutionary history of each assemblage before making conservation decisions, mainly for the Neotropical fish fauna, known to present high levels of specialization.

The number of words in the Abstract: 216

The number of words in main body of the paper, from the Introduction through the Biosketch: 3570

Number of references: 60

INTRODUCTION

Numerous debates within Ecology and Biogeography have investigated the influence of contemporary and historical factors on the structure of biological assemblages (Ricklefs, 2004). The absence of studies that integrate these two factors (Harrison et al. 2006) and the consideration that historical factors cannot be empiric tested (Francis & Currie, 1998), making more difficult to identify which one is most important. Patterns of species richness at continents are the main subject investigated in this type of study (Brown, 2014; Passy, 2009). In contrast, understand how the functional dissimilarity of assemblages is affected have received less attention (Violle et al. 2014).

The main hypothesis related with functional dissimilarity is the habitat template (Statzner and Bêche, 2010; Townsend & Hildrew, 1994). This theory predicts that contemporary conditions are more important than historical events (Poff et al. 1997). By this view, we can assume that two assemblages will be functionally similar according to the environmental similarity, independently of regional or historic factors. However, extrapolating these relations is not a straightforward task, given that innumerous filters may be operating and promoting complex assembly patterns (Jansson & Davies, 2008; Ricklefs, 2008; Tonn, 1990).

In South America, marine transgression (sea level has risen above 100 m) is one example of historical process that isolated fish faunas from two Brazilian biomes (Amazonia and Caatinga; Dias et al. 2014; Lovejoy et al. 2006; Ribeiro, 2006). Elevated regions of the Caatinga (humid forest enclaves), were not completely covered by the sea, acting as a natural refuge for the fauna in this biogeographic region. Subsequently, events of speciation and historical disturbances over time occurred in this biome (climatic changes and retraction forest; Tabarelli et al. 2004), promoting low taxonomic similarity with the Amazon region (Albert & Reis, 2011). In respect to biological diversity, the Amazonian biome is more diverse than Caatinga biome, due to its vast area, geological time and climatic stability (Peres *et al*., 2010). Thus, present-day patterns of functional dissimilarity between these two assemblages are probably product of the interaction of contemporary and historical factors.

Identifying the standards governing functional dissimilarity is of paramount importance for priority conservation areas (Olden et al. 2010; Villéger et al. 2011; Violle et al. 2014). Here, we will evaluate the importance of historical events and local conditions to functional dissimilarity diversity structure in Neotropical stream fishes. For this, we selected streams with similar environmental conditions in each biome. To better understand the factors that govern the functional dissimilarity, we first quantify the functional space (FRic) filled by each assembly and the amount of functional space not shared between the assemblies (F_{diss}). Second, we determined the influence of taxonomy richness on the observed FRic. Third, we determined the contribution of species (functional uniqueness; F_{uniq}) order to patterns of FRic and F_{diss}, allowing us to identify whether their functional strategies are different between biomes. Given the importance of historical events in shape the local taxonomic and functional structure of assemblage (Ricklefs et al. 2006; Tonn, 1990), similar functional strategies between assemblages should be higher in the same biome. In addition, we expected that the functional richness and dissimilarity patterns between biomes are explained by different levels of the functional uniqueness of the species because the complex system of environmental filters operating at different spatial and temporal scales can promote unique patterns of diversification (Ernst et al. 2012). To test these assumptions, regional or intercontinental studies are indispensable (Cilleros et al. 2016).

METHODS

Data set

We used fish datasets of the Amazon and Caatinga streams from the Projeto Igarapés (http://www.igarapes.bio.br/) and of the Laboratório de Ecologia Aquática of the Universidade Federal do Ceará. In total, we use 52 stream fish assemblages (26 from the Amazonia and 26 from the Caatinga; Figure S1). In the Caatinga and Amazonia, half of the selected streams show low depth characteristics of the water column, pebbly bottom and dense canopy cover (CA-COV and AM-COV, respectively; Figure A1.1 and Figure A1.2). The other half are composed of streams with sandy bottom characteristics, high depth of the water column and absence of canopy cover (CA-UNC and AM-UNC; Figure A1.1 and Figure A1.2). For streams, selection details and resume of environmental conditions see Appendix 1.

The same sampling protocol was carried out in all streams, where 50-m sections were sealed at the ends by locking nets to prevent fish from escaping. Within the 50-m stretch, four equidistant transects were determined, where the physical measurements of the streams (main channel width, mean depth, stream velocity, canopy cover and substrate type) and physicochemical (temperature, pH and dissolved oxygen) were measured (Mendonça *et al*., 2005). Subsequently, the ichthyofauna was sampled in all habitats available within the 50-m stretch with the use of trawls, sieves, and seine nets. Collecting and euthanizing fishes were done under collecting permits from IBAMA and institutional committees for ethics in research with animals. Voucher specimens were deposited at the fish collections of Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Amazonas state) and Universidade Federal do Rio Grande do Norte (Natal, Rio Grande do Norte state), Brazil.

Functional traits and multifunctional space

To characterize fish assemblages, an ecomorphological analysis were performed and a set of morphometric measures was taken in five adult individuals of each species. Subsequently, combinations of these morphometric measures (Table A2.1) generated 15 functional attributes. The selected morphological attributes will represent a proxy of locomotion capacity, food acquisition, and position in the water column, important components of the ecological niche of fish species (Violle et al. 2007).

Here the functional diversity was determined from the functional space occupied by each assembly within the multifunctional space constructed from the functional traits (Cornwell et al., 2006). To construct the multifunctional space, the 15 ecomorphological attributes were initially centered on zero mean and one standard deviation. Subsequently, a Principal Component Analysis (PCA) was performed to reduce the dimensionality of the data in the multifunctional space (Villéger *et al*., 2008). The distance between species in the multifunctional space is related to their functional similarities; the closer, the more functionally similar (Villéger *et al*., 2008).

From the multifunctional space obtained from PCA, we used the protocol developed by Maire et al. (2015) to determine the number of axes to be used to calculate diversity and functional dissimilarity between assemblages. This technique consists in correlating the distances of the species in the multifunctional space with the distances of the original matrix, to verify the congruence between the original data and those generated by the ordination techniques.

Functional indices

We quantify the volume of convex hull (Cornwell et al. 2006) occupied for each assemblages, using the number of PCA axes selected by the Maire et al. (2015). High convex hull values indicate assemblages with high diversity of the functional strategies (high functional richness, FRic). Because their values depend on the functional space of each assemblages in relation to the total volume, we standardize the FRic value by dividing by the value occupied by all the assemblages. Thus, FRic values range from zero for assemblages with low amplitude of functional strategies to one for assemblages with high amplitude of functional strategies (Villéger et al. 2008).

The functional dissimilarity (F_{diss}) represents the replacement of functional strategies between two or more assemblages (Villéger *et al.*, 2011). F_{diss} is equal to the ratio between not shared and total functional space, following the formula below:

$$Fdiss = \frac{2 * \min(b, c)}{a + 2 * \min(b, c)}$$

Where a is functional volume (FRic) shared by the two assemblages and b and c the unique functional volume filled for the two assemblages (Villéger *et al.*, 2011). F_{diss} varies between zero, when two assemblages are completely similar, to one when two assemblages are completely overlapping in functional space. As the F_{diss} is highly dependent on the extent of functional space filled by assemblage, F_{diss} values were standardized against the total volume occupied by the two assemblages (Villéger *et al.*, 2011).

Statistical analysis

We used null models to test whether the observed FRic and F_{diss} values are significantly different from expected at random. The species richness of each assemblages were kept constant, while the functional identity of the species was randomly distributed (Villéger *et al*., 2013). For each pair of assemblages, 999 null models were generated and the simulated FRic and F_{diss} values computed. The standardized effect size (SES) was used to measure the difference between observed values (obs) and null expectation (rand): SES = $FRic_{obs}$ – mean ($FRic_{rand}$) / sd ($FRic_{rand}$). When the $FRic_{obs}$ is less than 2.5% of the simulated values, the functional richness of the assemblages is considered clustered, on the other hand, if the $FRic_{obs}$ is greater than 97.5% of the simulated values functional richness of the assemblages is overdispersed. For F_{diss}, if the observed value is less than 2.5%, we will assume that the two assemblages present similar functional strategies (high overlap), but if the observed value is greater than 97.5%, we will assume that the two assemblies have different functional strategies). As the number of species varies between groups we compute the value of FRic after performing a bootstrap technique (N = 10,000) based on the smallest number of species within the four groups.

We used the functional uniqueness of the orders of fish (F_{uniq}; Toussaint et al., 2016). For the calculation of F_{uniq} the Perciformes, Cyprinodontiformes, Gymnotiformes and Synbranchiformes were treated as "Others" because they presented few species per stream group. The functional uniqueness of each represent the proportion of the functional space filled only the order considered:

$$Funiq = \frac{(a_r^o)}{(a_r^o + b_r^o)}$$

Where, a_r^o is the volume of order filled only the order *o* while b_r^o is the volume shared with all orders present in assemblage. From this index, we can identify if species of the same order present different functional strategies between and within biomes. High values of F_{uniq} indicate that species of a certain order use different functional strategies in a particular assemblage that are not shared by species of the same order in other assemblages.

All analyses to get to the functional indices were computed using the function *functional.beta.core* from betapart R package (Baselga and Orme, 2012). All statistical analyses were carried in R version 3.3.0 (The R Foundation for Statistical Computing).

RESULTS

Functional richness and dissimilarity

The database includes 122 species belonging to six orders. Four PCA axes were selected by the Maire et al. (2015) protocol. CA-COV and AM-COV filled respectively 10% and 17% of functional space available whereas CA-UNC and AM-UNC filled respectively 30% and 78% of functional space of all functional volume available (Table 1; Figure 1; Figure A3.1). Both stream groups had not significantly lower FRic than expected by chance given their respective taxonomic richness (Table 1). However, it is important mentioning that COV streams had lower SES values than UNC streams, suggesting less increase of functional richness with increase of taxonomic richness. The FRic of UNC streams were not significantly different than expect by chance given the taxonomic richness of stream groups, and hence the functional difference observed between the streams groups were due to a species richness effect (Table 1).

In terms of functional dissimilarity, the more similar assemblages shown high environmental similarity (Table 2). The smallest functional dissimilarity was observed between COV values (CA-COV and AM-COV; Table 2). However, different from our predictions, none of dissimilarity values was significantly greater than expect after controlling the taxonomic richness ($-0.90 < SES > 1.10$; Table 2).

Contribution of the species of each order to the functional richness

The functional space was dominated for two Orders (Characiformes and Siluriformes) which filled 40.8% of functional space available (Figures S3.2). These high values of FRic was dependent of species richness (Spearman's rank correlation rho = 0.61, $n = 12$, $P = 0.03$). For all streams, the functional uniqueness of the orders also showed high correlation with the species richness (Spearman's rank correlation rho = 0.89, $n = 12$, $P < 0.001$, respectively). Together, these results suggests that the increasing of species promotes more filling functional space via specialization of functional strategies and that the Orders of each assemblage feature distinct functional strategies (high values of F_{uniq}; Figure 2; Table 3).

DISCUSSION

The idea that local are dependent on regional processes have been debated for decades (Ricklefs, 1987; Tonn, 1990). Understanding the balance between these two factors is of extreme importance not only to identify the patterns that govern biodiversity but also to develop correct conservation strategies (Chase & Leibold, 2003; Ellis, 2015; Fukami, 2015; Olden et al. 2010). We used fish assemblages from two biomes of South America, which different evolutionary histories to evaluate the balance between local contemporary and historical/evolutionary forces (Figure 3). The historical filters selected the species pool of each biome capable of colonizing local assemblies (Figure 3A, B). Properties of local habitat filtered the species more adapted to environmental conditions (Figure 3C, D). In particular, compressed and deep body shapes, large eyes, compressed caudal peduncle, terminal to superior mouth position and large head (such as Characiformes and Perciformes) were more associated with UNC streams (Figure 3; Figure S2). Conversely, species with long peduncles, dorsal and small eyes, inferior mouth and depressed body, as such, the armored catfishes (Siluriformes) had mode importance in COV streams (Figure S2). Despite this strong relation between functional characteristics of the species and contemporary factors, high F_{uniq} values were observed. One of the possible explanations is the difference in the pool of species capable of colonizing local assemblages, generated by historical filters. As an example, we have the species of the order Characiformes, which despite having characteristic body patterns have different strategies between and within each biome (Table 3).

The joint action of historical and local factors

Historical events that occurred in South America are among the major drivers of biodiversity distribution (Hubert & Renno, 2006). Coupled with large diversification time, they promoted higher diversification and innumerable areas of endemism (Gaston & Blackburn, 1996; Hubert & Renno, 2006). In despite of these patterns, we find that local conditions are more important in explaining patterns of functional richness and dissimilarity, when the taxonomic richness is controlled (Townsend & Hildrew, 1994). However, high values of functional singularity suggest that the differentiated selection of the species pool by historical factors represents an important structuring agent of local assemblies (Ricklefs, 2011). Our results suggest that the combination of contemporary and historical events generate idiosyncratic patterns in fish assemblages, reinforcing the importance of investigating how historical filters influence the local patterns of assemblages.

Contemporary factors were the main responsible for taxonomic and functional richness patterns. In open canopy streams, highest FRic values were explained by the presence of species with extreme traits combinations (Figure A3.1; Figure A3.2). One of the possible explanations for this pattern is the relatively higher productivity in these environments promoted by the high concentration of macrophytes (Sand-Jensen et al. 1989; see Figure A1.1). In fact, the high spatial heterogeneity promoted by macrophytes function as refuges and source of reproduction and food for many fish species (Teixeira-Melo et al. 2015). The patterns of dissimilarity also revealed greater importance of local conditions, despite the low statistical significance. Evolutionary divisions of fauna during historical events may be one of the reasons for the low significance of these results, generating lineages of different species between assemblies, but converging within similar environments (Ricklefs, 2007). Thus, the contemporary events can be treated as modelers of historical events.

Combination between contemporary and historical factors in explaining local patterns was also observed in intercontinental studies of anuran assemblages (Ernst et al., 2012) and of coral reef fish (Bender et al. 2013; Leprieur et al. 2015). However, from the investigation of the functional relationship between species we demonstrate the importance of each of these factors in structuring streams fish assemblages. These results are in agreement with the unidirectionality mechanism that historical and contemporary abiotic filters have in composing local assemblies (Toon, 1990; Ricklefs, 2004). Cilleros et al. (2016) observed a practical example of the joint importance of historical and local events. In their study, the authors identified different patterns of functional dissimilarity between temperate and tropical fish assemblages, explained by contemporary and historical factors. The interpretation of the results presented in this study together with these evidences of the literature, point out that the balance between historical forces and contemporary places is more complex than predicted by the great theories of assembly structure (Poof et al. 1997; Townsend & Hildrew 1994). Thus, we demonstrate support for Ricklefs's (2004) claim that contemporary and historical factors interact continuously in time and space, and that both create unique patterns for each local assemblage. This alerts us to the specificity that future management plans in certain areas aim to maximize the contemplated biodiversity.

In the ecological and biogeographical literature are not there a consensus about the existence of idiosyncratic patterns. Winemiller (1991) and Leprieur et al. (2011) not found evidence for idiosyncratic patterns, while Strauss (1989) and Ernst et al. (2012) demonstrate that the assemblages of ichthyofauna and anuran showed different functional strategies between continents. The biogeographic location where the studies were performed (hemispheres south or north of the earth), represents one of the main explanations for these divergent results. The northern hemisphere was the target of large glaciations, which promoting less time of speciation and generated nested assemblies of regions not frozen (Dobrovolski et al., 2012). These regions present great dependence of a great historical event, what causes homogenization and low richness of species at the regional level (Villéger et al., 2013). On the other hand, glaciations had little effect on biological assemblies in the northern hemisphere allowing more time for speciation (Peres et al., 2010) and more interactions between species and contemporary factors. Thus, time is an important variable that may be linked to idiosyncratic patterns. Assemblies that present historical filters very early in their evolutionary history have higher rates of specialization due to adaptation to contemporary conditions.

The capacity of particular adaptations of groups of species to affect biodiversity patterns between (Fukami et al., 2005; Ricklefs, 2007) and even within the same region is well known (Hawkins et al. 20005). In our study, such adaptations were mainly responsible for rejecting the hypothesis of habitat template. Moreover, the positive relationship between taxonomic and functional richness suggests that assemblages showed relatively low functional redundancy in Neotropical stream fishes. These results alert us to the importance of conservation of this Neotropical fauna, even in places that do not have high species richness (Vitule et al. 2017). For instance, Caatinga biome harbors less species compared with Amazonian biome, but Caatinga has high rates of endemism (Rodrigues-Filho 2016).

How do anthropogenic disturbances relate to idiosyncratic patterns?

Although our results are interpreted in such a way that local filters are able to select only the species already selected by historical filters, anthropic disturbances can affect the unidirectionality of this relation inserting more complexity to the system. Local extinction via habitat degradation and species introduction may be examples of anthropogenic disturbances that directly affect the functional structure of these assemblages by compromising the hierarchical network of ecosystem services (Dala-Corte et al. 2016; Hefferman et al. 2014; Mouillot et al. 2011; Mouillot et al. 2013). Such disturbances present a threat to the unique patterns of functional biodiversity promoted by historical and contemporary factors (Villéger et al. 2014). Habitat degradation is closely linked with increased functional redundancy within assemblies by removing species with functional traits that are poorly adapted to environmental changes (Casatti et al. 2015). This functional simplification increases the invasion success of alien species by increasing the number of niches available within assemblies (Mouillot et al. 2013; Speek et al. 2014). The taxonomic and functional homogenization promoted by these species introduction is, even more, warning for the Neotropical fish fauna due to its high presence of endemic species that are mostly listed as vulnerable to extinction (Vitule et al. 2016). These considerations emphasize the need to understand the mechanisms of local and regional biodiversity. Specifically, in the Caatinga biome, these human interventions are more evident than in the Amazonian biome, which still presents well-preserved regions. In this biome, due to actions of fish farming and aquariums, numerous introduced species are promoting extinctions of native species (Malthcik & Medeiros, 2012).

CONCLUSIONS

Beyond their conceptual importance, understand the factors that influence the functional biodiversity are also important in conservation context (Olden et al. 2010). Here, we find that historical and environmental conditions exert combination influence on the functional structure of Neotropical stream fish assemblage. Such a joint action may be one of the possible explanations for the great controversy of current studies that directly or indirectly test the habitat template premises without taking into account the evolutionary history of the assemblies. This is especially important to conservation given the crescent advance of anthropogenic changes in the most diverse ecosystems of the earth (Cardinale et al. 2012; Jackson et al. 2001). The high functional specialization and the idiosyncratic pattern associated with the increasing wave of anthropic disturbances alert us to future research investigating the consequences of anthropic impacts on the erosion of functional diversity in the resistance of the congregation to biological invasions (Speek et al. 2014).

ACKNOWLEDGEMENTS

We are grateful to the Brazilian National Research Council (CNPq) funded this research. JZ receives a productivity grant from CNPq (#313183/2014-7). The study was funded by CNPq/PPBIO through grant #457463/2012-0 and by CNPq/ICMBio through grant #552009/2011-3. Also thanks to the Ministry of the Environment (MMA; 26174-2) and the Chico Mendes Institute for Biodiversity Conservation (ICMBio/SISBIO; 32921-4) for granting licenses to collect fish samples.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Geographic locations of sampled points

Figure S2 Relative proportion of species in each fish order

Appendix S1 Selection of streams with similar environmental conditions and heterogeneity

Appendix S2 Functional trait assessment

Appendix S3 Multifunctional space

BIOSKETCH

Carlos Rodrigues-Filho is interested in understand the relation between local and regional forces that shape the functional structure of biological assemblages. This article is a product of Rodrigues-Filho's MSc thesis, conducted at the Ecology Graduate Program of Brazil´s National Institute for Amazon Research (INPA).

Table 1 Number of species (Nb. of species), observed values (mean of simulated) FRic, standardize effect (SES), probability associate with null models (P) and bootstrapped FRic values (95% confidence interval).

	Nb. of species	FRic observed (%)	SES	*P* value	$Boot_{n=20}$	$Boot_{n=24}$	$Boot_{n=32}$
CA-COV	20 (16.3%)	0.10 (0.17)	-0.99	0.11	-	-	-
CA-UNC	32 (26.2%)	0.30 (0.32)	-0.07	0.55	0.04-0.27^{ns}	0.08-0.29^{ns}	-
AM-COV	24 (19.6%)	0.17 (0.23)	-0.91	0.18	0.10-0.17^{ns}	-	-
AM-UNC	77 (63.1%)	0.78 (0.70)	0.60	0.73	0.06-0.38^{ns}	0.09-0.46^{ns}	0.17-0.56^{ns}

^{ns}non significant values based in 10,000 bootstrapped.

Table 2 Functional dissimilarity between groups.

Streams groups	F_{diss} (%)	SES	*P* value
CA-COV vs. CA-UNC	68	0.24	0.56
CA-COV vs. AM-COV	57	-0.90	0.17
CA-COV vs. AM-UNC	87	1.10	0.87
CA-UNC vs. AM-COV	61	0.25	0.68
CA-UNC vs. AM-UNC	69	0.75	0.74
AM-COV vs. AM-UNC	79	1.05	0.85

Functional dissimilarity values (F_{diss}) between pairs of groups. Associated P-values obtained under the null model (N = 999) are provided in parentheses.

Table 3 Functional space filled (FRic) and uniqueness (F_{uniq}) of each order for covered (COV) and uncovered (UNC) streams and. Values in parentheses representing the richness of species in each order. Due to computation constraints, the functional space of orders with less five species was not measured (-). “Others” include the orders Perciformes, Cyprinodontiformes, Gymnotiformes and Synbranchiformes.

	All groups		CA-COV		CA-UNC		AM-COV		AM-UNC	
	FRic	F_{uniq}	FRic	F_{uniq}	FRic	F_{uniq}	FRic	F_{uniq}	FRic	F_{uniq}
Characiformes	28.08 (63)	27.57	0.13 (8)	0.00	0.80 (19)	0.68	0.13 (9)	0.00	3.88 (43)	2.90
Siluriformes	42.63 (24)	22.25	0.02 (6)	0.01	0.03 (6)	0.01	0.05 (6)	0.04	2.50 (13)	1.97
Perciformes	7.33 (15)	1.18	-	-	-	-	-	-	0.27 (9)	0.13
Cyprinodontiformes	0.11 (7)	0.11	-	-	-	-	-	-	-	-
Gymnotiformes	0.09 (11)	0.08	-	-	-	-	-	-	0.01 (10)	0.01
Synbranchiformes	-	-	-	-	-	-	-	-	-	-
Others	62.92 (35)	49.91	0.28 (5)	0.06	0.99 (6)	0.61	0.55 (9)	0.02	6.20 (21)	4.64

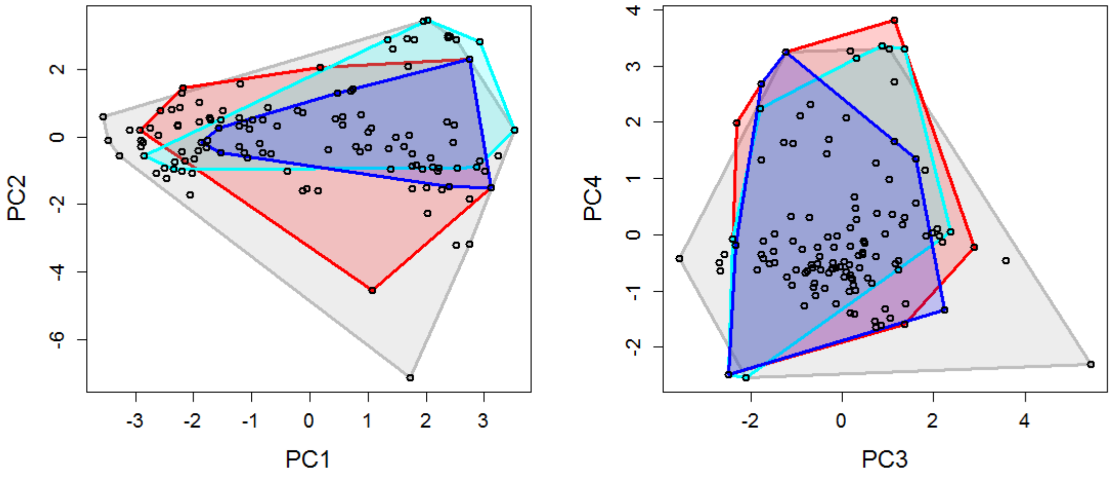

Figure 1 Functional space built with the species pool of covered and uncovered streams from the Caatinga and Amazonia biomes (see Figure A3.1 for PC all combinations). (blue) CA-COV; (cyan) AM-COV; (red) CA-UNC; (gray) AM-UNC. Lines representing the convex hulls volumes of each stream group.

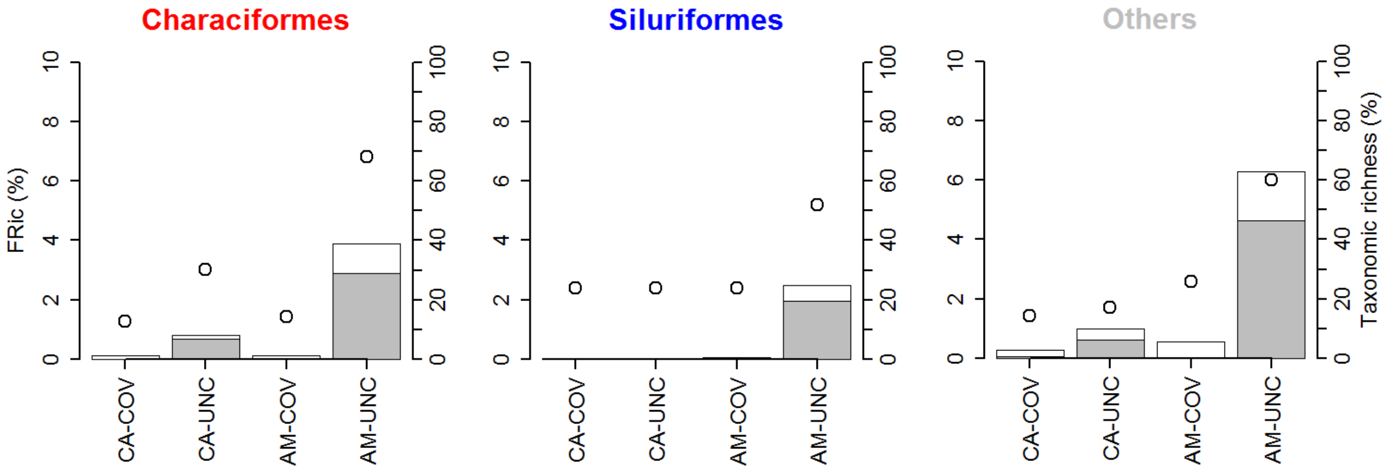

Figure 2 The functional richness of each order in each assemblage is given as the percentage of all assemblages FRic (white bars). Gray bars represent the functional uniqueness (Funiq) of each order. Circles represent the relative proportion of taxonomic richness of each order in each assemblage given the total species number.

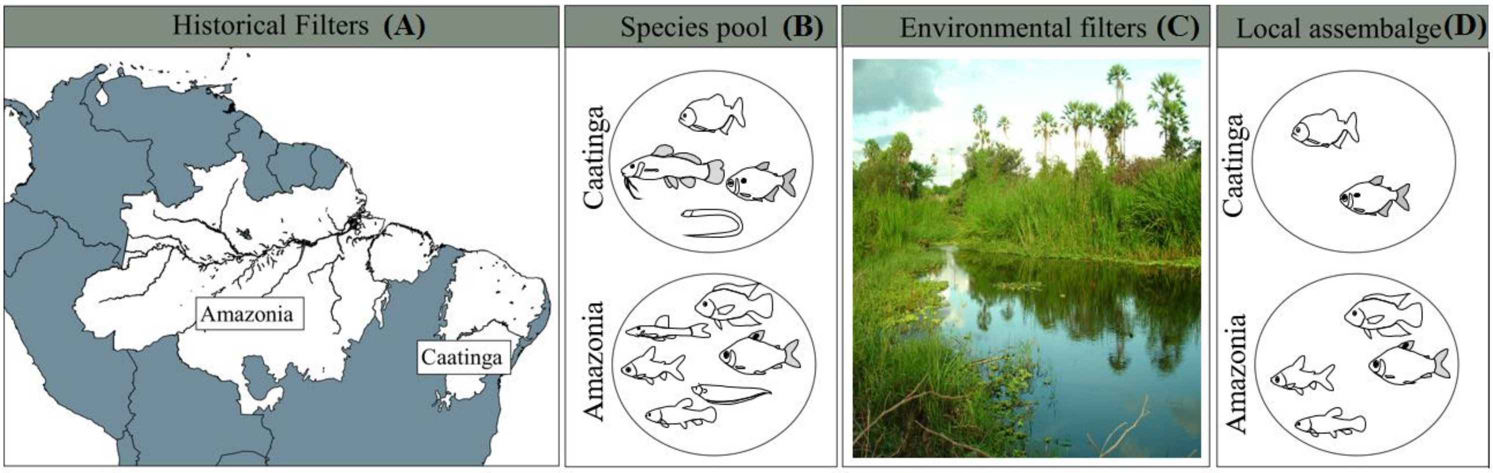

Figure 3 Summary balance between historical and local drivers in functional structure of fish assemblage. Historical filters are responsible for selecting the species pool in each biome. Then local filters select the species most adapted to the habitat characteristics, however, an identity of the species selected by historical filters is maintained. Thus, the local assemblies are derived from historical and local filters, promoting unique standards in each assembly.

Síntese

As crescentes modificações antrópicas nos mais variados ecossistemas da terra têm afetado diretamente a dinâmica de assembleia ecológicas (Mouillot *et al*., 2013). Tal intervenção tem promovido erosões na biodiversidade principalmente por eliminar espécies raras, mas que possuem elevada importância ecológica para o funcionamento de ecossistemas (Leitão *et al*., 2016; Mouillot *et al*., 2011). Isso ocorre pois existe uma íntima relação entre as características funcionais das espécies com as características do hábitat (Díaz & Cabido, 2001), o que gera graves consequências em eventos de perda de hábitat.

Mostrei nesse trabalho que fatores históricos são importantes modeladores dos padrões atuais de especialização e redundância funcional em peixes de riachos e que em conjunto com fatores contemporâneos são responsáveis por governar a estruturação de assembleias locais de peixes de riachos de dois biomas do Brasil (Caatinga e Amazônia). Em adição, os padrões idiossincráticos observados na literatura, podem ser derivados do tempo em que o último grande evento histórico ocorreu. Como exemplo maiores casos de padrões idiossincráticos são observados em regiões Tropicais em detrimento de regiões Temperadas, a qual apresentaram eventos recentes de glaciação que são os principais responsáveis pela distribuição atual de espécies na região (Dobrovolski *et al*., 2012). Esses resultados foram comprovados (i) maior importância de espécies redundantes no bioma Caatinga, que apresentou inúmeros distúrbios históricos ao longo de seu processo evolucionário (ii) assembleias localizadas em riachos com condições semelhantes, independentemente do bioma, apresentaram valores de riqueza e dissimilaridade funcional similares. No entanto, a diferença do pool de espécies decorrente de processos históricos é responsável pelos altos valores de singularidade funcional das espécies (forças responsáveis por gerar padrões idiossincráticos).

Nesse trabalho a composição de espécies entre a Amazônia e Caatinga apresentaram apenas seis espécies em comum, em um total de 122. Esse panorama torna comparações entre biomas bastante inacessíveis. A utilização da abordagem funcional, por outro lado, é capaz de comparar assembleias completamente diferentes taxonomicamente. Utilizamos essa característica da diversidade funcional para mostrar que grandes distúrbios podem causar severas perda de especialização funcional em assembleias de peixes de riachos. Além de distúrbios de larga escala, a íntima relação entre a diversidade funcional e as condições locais nos alertam que pequenas modificações também possuem potencial de afetar diretamente a estrutura de assembleia de peixes de riachos.

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APÊNDICE A – MATERIAL SUPLEMENTAR DO MANUSCRITO EM ETAPA DE SUBMISSÃO PARA *Functional Ecology*

Functional Ecology

SUPPORTING INFORMATION

Historical disturbances promote high redundancy and low functional specialization in Neotropical fish assemblage

Carlos A. S. Rodrigues-Filho, Rafael P. Leitão, Jansen Zuanon, Jorge I. Sanchéz-Botero and Fabricio B. Baccaro

Appendix S1 Selection of streams with similar environmental conditions and heterogeneity. For selecting streams with similar environmental conditions and heterogeneity between Amazonia and Caatinga, we performed exploratory analyses of PCA (for visualization of results), permutational multivariate analysis of variance (PERMANOVA) and homogeneity of multivariate dispersion based on the centroid (PERMDISPER; Anderson, Ellingsen & McArdle 2006). Initially a PCA was carried out with the whole set of Caatinga streams (40) and a similar set for Amazonia (45). The points with the highest environmental values (high loadings values) were visually selected and extracted, and then 20 streams of each region were selected (Fig. A1). Among the two groups, no differences in conditions (PERMANOVA; F38,2 = 1.8 and P = 0.1) and environmental heterogeneity (PERMDISPER; F38,2 = 0.0019 and P = 0.955) were observed.

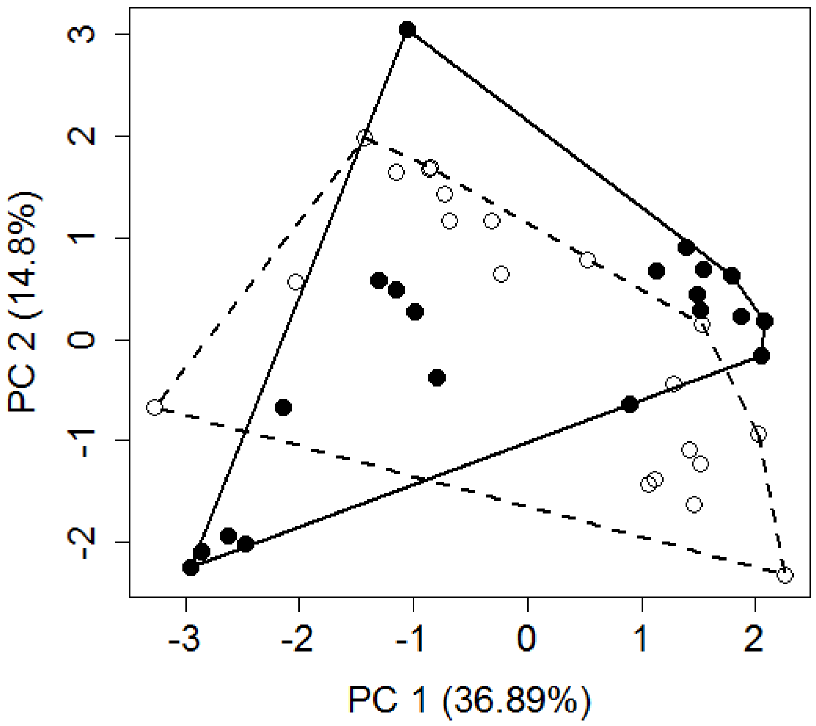

Fig. S1.1 PCA of the environmental conditions of the streams based on a Pearson correlation matrix. (●) Amazonia; (○) Caatinga.

Appendix S2 Functional trait assessment

From the ecomorphological analysis (20 measures; Fig. S2.1), we obtained 15 functional traits (Table S2.1) related to locomotion capacity, food acquisition and water column position for 109 species (q.v. Leitão et al. 2016).

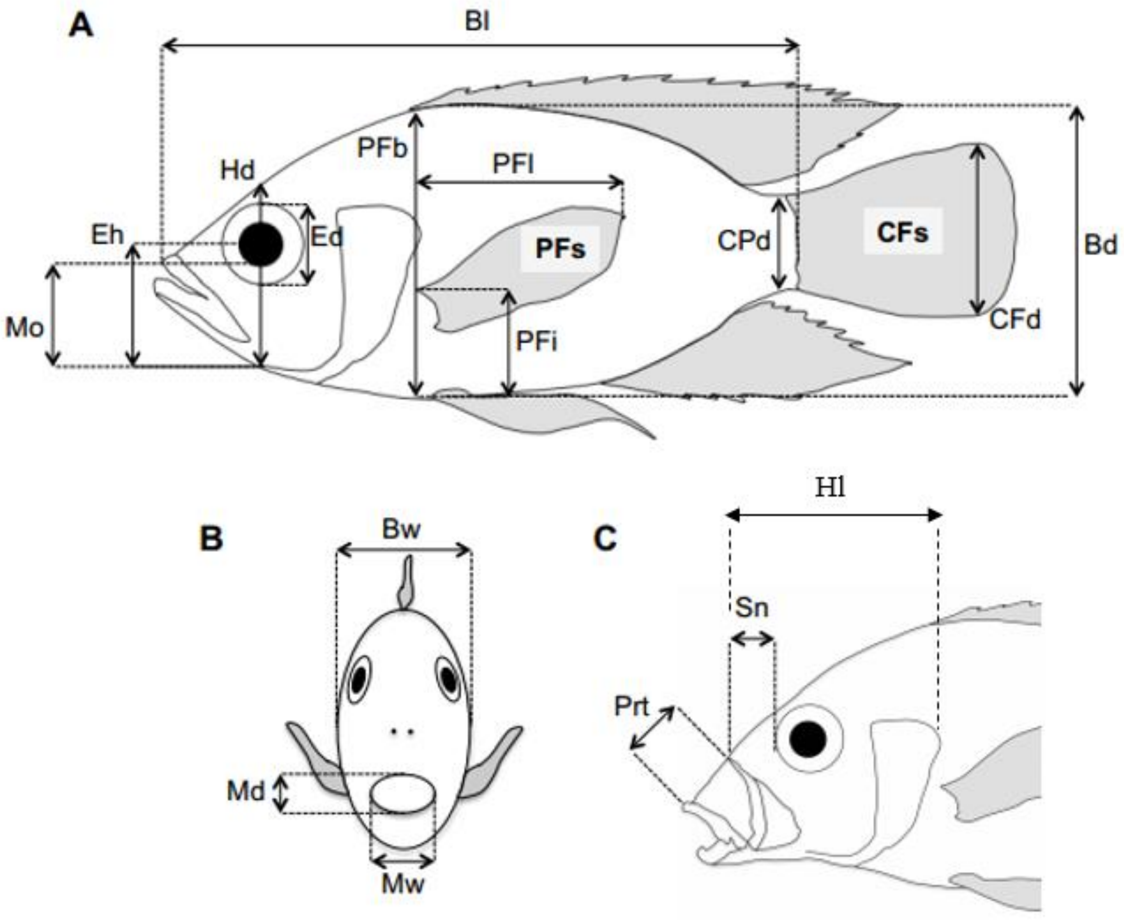

Fig. S2.1 Nineteen morphological traits measured for fish on digital pictures (A): *Bd* body depth, *CPd* caudal-peduncle minimal depth, *CFd* caudal-fin depth, *CFs* caudal-fin surface, *PFi* distance between the insertion of pectoral fin to the bottom of the body, *PFb* body depth at the level of the pectoral-fin insertion, *PFl* pectoral-fin length, *PFs* pectoral-fin surface, *Hd* head depth along the vertical axis of the eye, *Hl* length of the head, measured from the muzzle tip to the most posterior end of the operculum, *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 indexes measured from the ecomorphological traits of the species. 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 *et al.*, 2010
Pectoral-fin position	$\frac{PFi}{PFb}$	PFps	Pectoral fin use for maneuverability	Dumay *et al.*, (2004)
Aspect ratio of the pectoral fin	$\frac{PFl^2}{PFs}$	FPar	Pectoral fin use for propulsion	Adapted from Fulton *et al.*, (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 *et al.*, 2010
Fins surface to body size ratio	$\frac{(2 * PFs) + CFs}{\frac{\pi}{4} * Bw * Bd}$	Fsf	Acceleration and/or maneuverability efficiency	Villéger *et al.*, 2010
Body mass	$\log(Massa + 1)$	LogM	Metabolism, endurance and swimming abilit	Villéger *et al.*, 2010

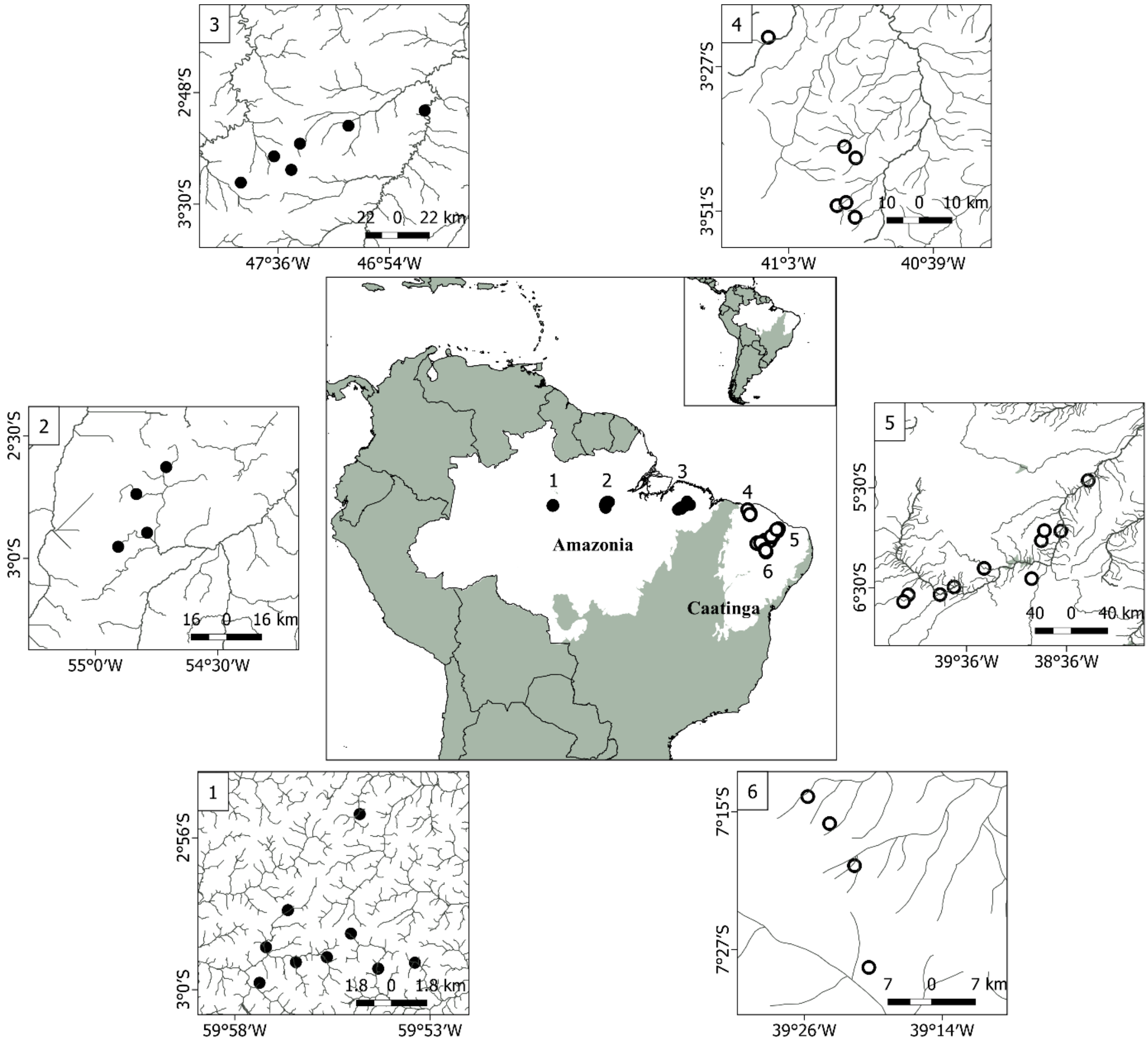

Fig. S1 Geographical locations sample for Amazonia and Caatinga biomes. In each biome, 26 points were sampled. (●) Amazonia; (○) Caatinga.

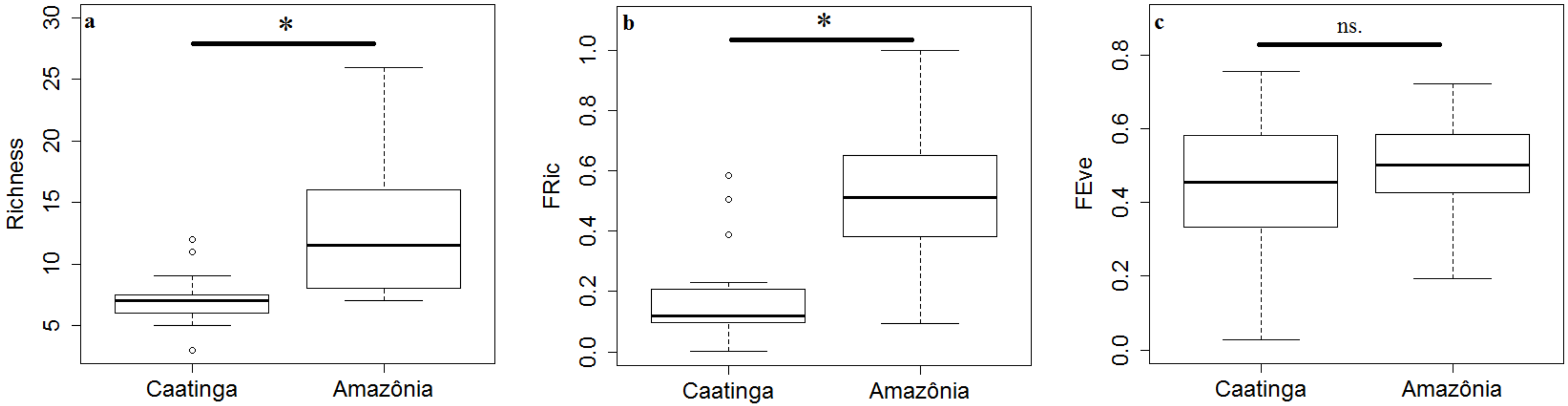

Fig. S2 Summary of species richness (a), Functional Richness - FRic (b) and Functional Evenness - FEve (c) for local stream fish assemblages of Caatinga and Amazonia. Significant differences between the two biomes were accessed by t-test, assuming α = 0.05. (*) Significant differences; (ns.) Non-significant differences. Outliers are represented by white dots.

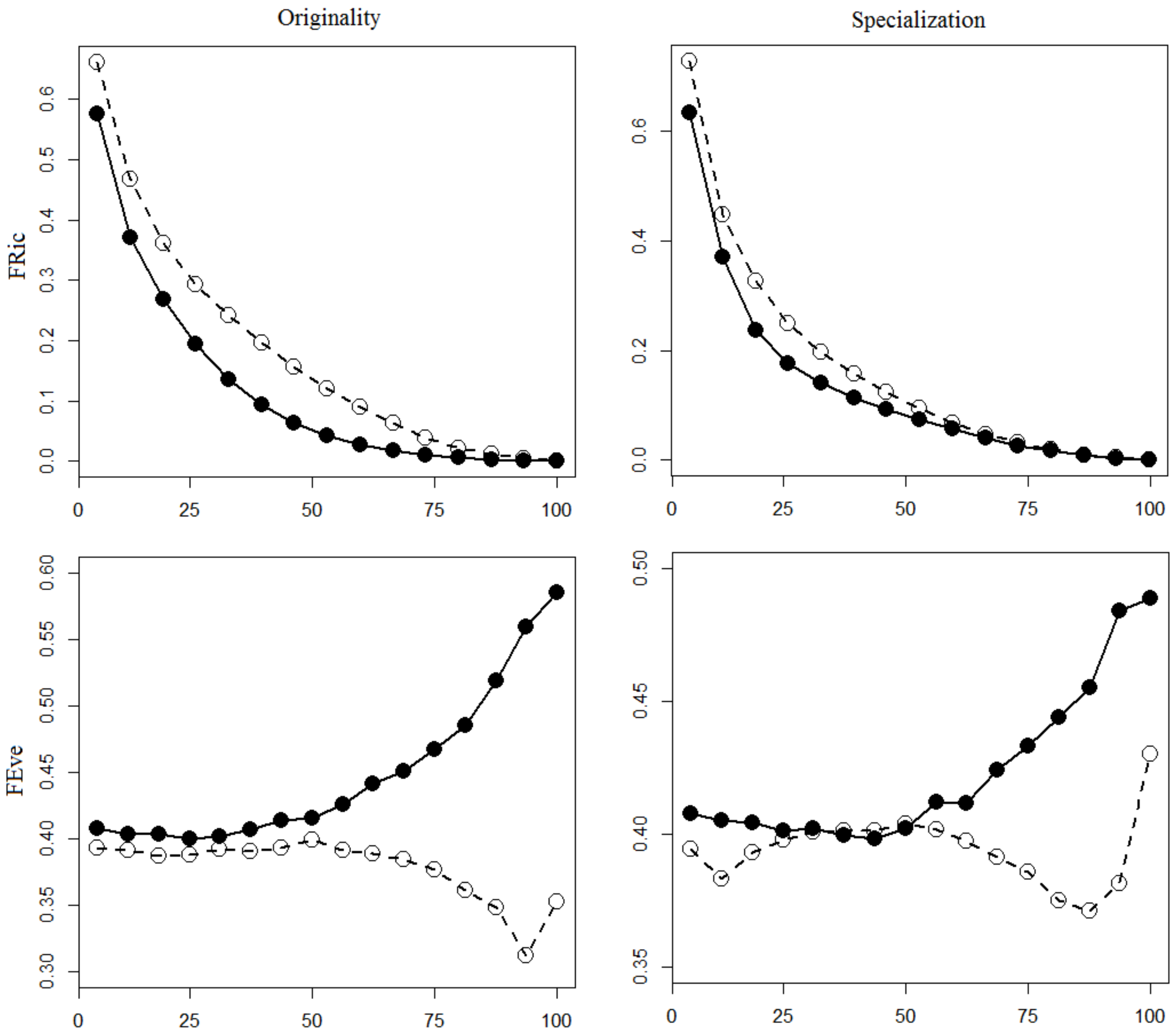

Fig. S3 Comparison of the effects of species losses ordered by the functional originality (FOri) and specialization (FSpe) of the species to 1,000 subsamples of 20 species from stream fish assemblies from Amazonia (●) and Caatinga (○). Each point represents the median value of the 1,000 values of Functional Richness - FRic and Functional Evenness - FEve remaining after species loss.

APÊNDICE B – MATERIAL SUPLEMENTAR DO MANUSCRITO EM ETAPA DE PREPARAÇÃO PARA *Diversity and Distributions*

Diversity and Distributions

SUPPORTING INFORMATION

The joint action of historical and local factors are responsible for generating idiosyncratic patterns in fish assemblages

Carlos A. S. Rodrigues-Filho, Rafael P. Leitão, Jansen Zuanon, Jorge I. Sanchéz-Botero and Fabricio B. Baccaro

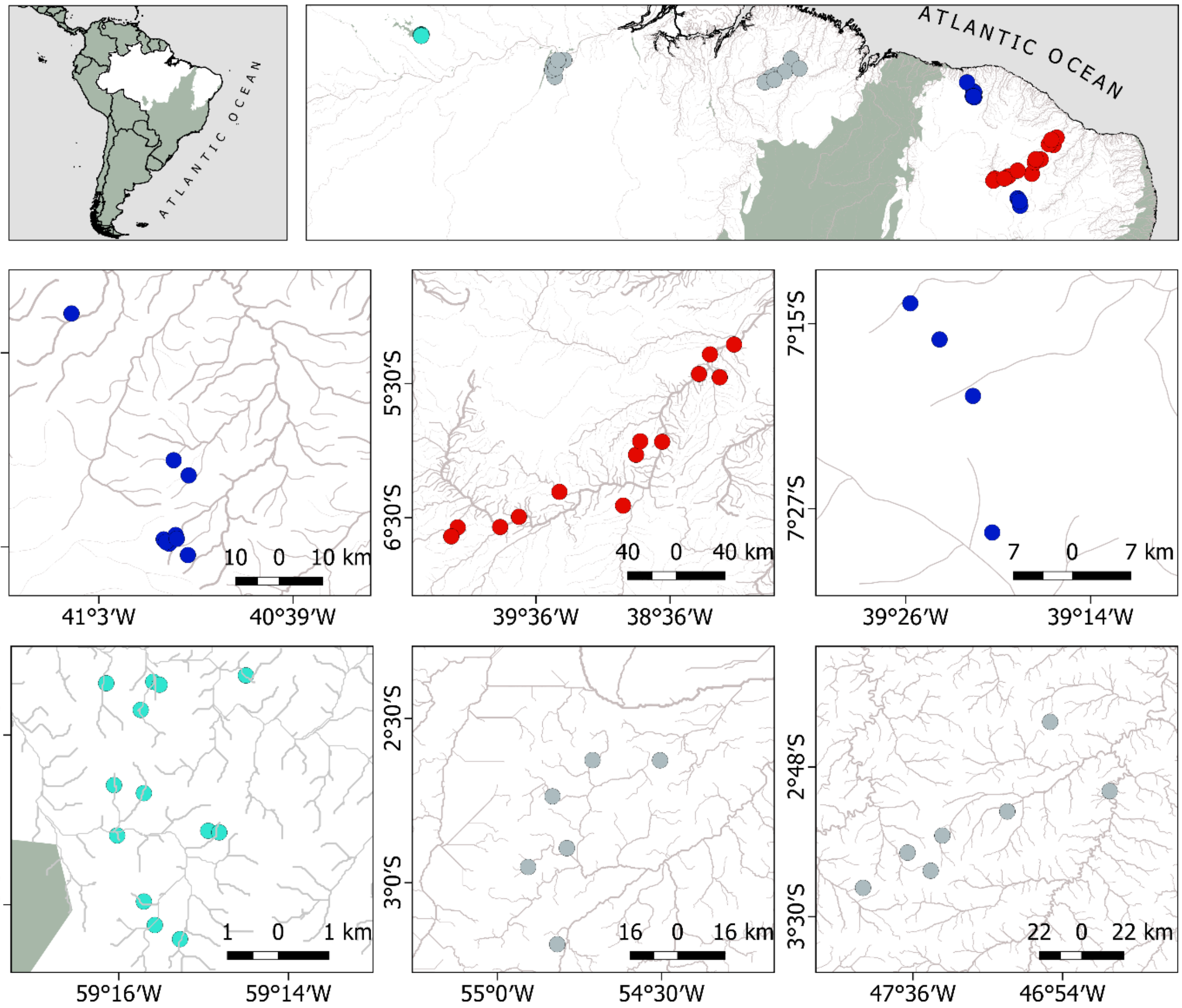

Figure S2 Geographic locations sampled for Caatinga (26plots) and Amazonia (26 plots). (blue and red) Caatinga; (cyan and gray) Amazonia. We followed the east-west orientation in the subdivisions of the map.

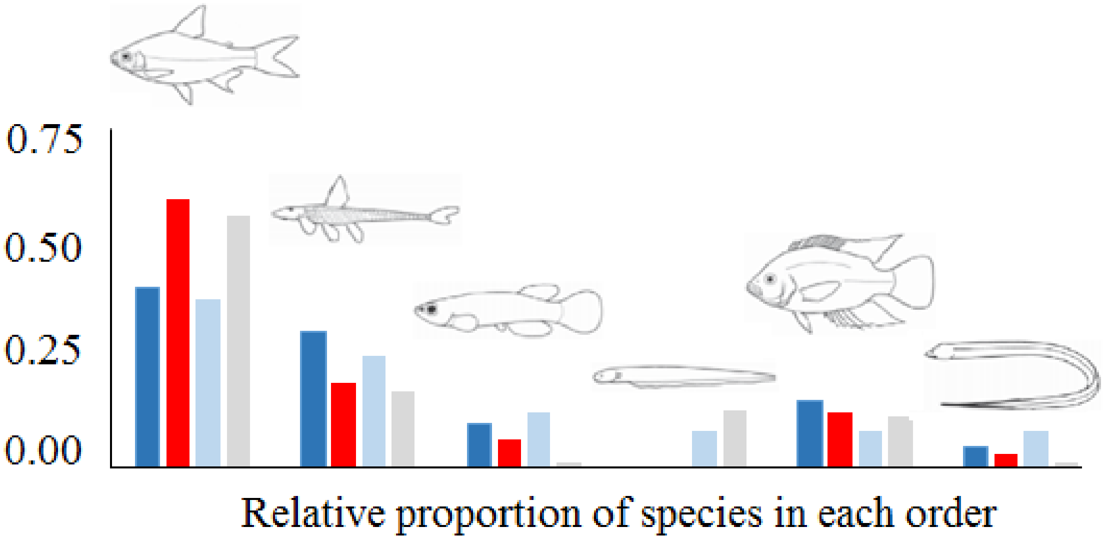

Figure S2 Relative proportion of species in each order in CA-COV (blue), AM-COV (cyan), CA-UNC (red) and AM-UNC (gray) streams.

Appendix S1 Streams selection.

From the data set of Aquatic Ecology Laboratory-LEA (Caatinga) and Projeto Igarapés (Amazonia), we select 52 streams. The streams selection visually from the PCA analysis and based on environmental similarity in order to identify two distinct streams groups in each biome (Table A1.1; Figure A1.1). One of the groups is composed by the low depth of the water column, pebbly bottom and dense canopy cover, here denominate COVERED streams (COV; Figure A1.2a, b). The other group shown as a characteristic sandy bottom substrate, high depth of the water column and absence of canopy cover, here denominated UNCOVERED streams (UNC; Figure A1.2c, d).

Table A1.1 Resume of environmental conditions in each stream.

Biome	Group	VEL	WID	DEP	CAN	TEMP	pH	O2	P_G	SAN	S_C
Caatinga	CA-COV	0.32	5.42	0.21	1.00	23.50	8.10	9.20	0.30	0.59	0.11
Caatinga	CA-COV	0.39	4.78	0.41	1.00	22.00	7.80	7.50	0.57	0.39	0.02
Caatinga	CA-COV	0.17	3.53	0.10	1.00	23.50	7.60	9.20	0.42	0.56	0.01
Caatinga	CA-COV	0.42	7.52	0.06	1.00	27.00	8.70	12.20	0.71	0.23	0.04
Caatinga	CA-COV	0.14	5.71	0.33	1.00	22.50	6.80	8.80	0.29	0.64	0.06
Caatinga	CA-COV	0.28	4.80	0.14	1.00	26.00	7.50	8.90	0.37	0.61	0.01
Caatinga	CA-COV	0.35	4.15	0.06	1.00	24.70	6.50	11.50	0.55	0.29	0.15
Caatinga	CA-COV	0.22	1.89	0.21	1.00	23.30	6.80	9.60	0.47	0.32	0.20
Caatinga	CA-COV	0.39	4.52	0.23	1.00	23.00	8.02	13.00	0.53	0.26	0.20

Caatinga	CA-COV	0.14	3.32	0.26	1.00	26.20	7.80	9.50	0.44	0.53	0.02
Caatinga	CA-COV	0.18	2.82	0.16	1.00	23.00	6.80	7.80	0.49	0.17	0.33
Caatinga	CA-COV	0.17	1.66	0.15	1.00	23.50	7.30	12.30	0.45	0.50	0.04
Caatinga	CA-COV	0.31	4.68	0.21	1.00	26.00	7.90	12.50	0.23	0.73	0.03
Caatinga	CA-UNC	0.25	4.02	0.91	0.00	30.47	7.58	3.82	0.05	0.83	0.11
Caatinga	CA-UNC	0.01	7.50	0.42	0.00	26.73	7.12	4.35	0.40	0.20	0.40
Caatinga	CA-UNC	0.12	5.54	0.36	0.00	26.43	8.05	5.09	0.00	0.80	0.00
Caatinga	CA-UNC	0.01	10.29	0.23	0.00	26.27	7.80	3.50	0.10	0.70	0.20
Caatinga	CA-UNC	0.01	10.36	0.65	0.00	26.19	7.78	3.89	0.30	0.50	0.20
Caatinga	CA-UNC	0.19	7.25	1.29	0.00	27.40	6.96	5.53	0.00	0.50	0.50
Caatinga	CA-UNC	0.04	8.56	0.91	0.00	28.66	8.50	10.13	0.30	0.70	0.00
Caatinga	CA-UNC	0.06	8.00	0.97	0.00	27.98	7.49	2.62	0.00	0.30	0.70
Caatinga	CA-UNC	0.25	9.35	0.29	0.00	27.62	8.85	6.80	0.00	0.70	0.30
Caatinga	CA-UNC	0.22	7.75	0.27	0.00	29.21	8.79	7.58	0.00	0.70	0.30
Caatinga	CA-UNC	0.17	11.20	0.40	0.00	28.53	8.93	7.18	0.30	0.30	0.40
Caatinga	CA-UNC	0.22	8.35	0.50	0.00	28.38	8.95	8.57	0.20	0.60	0.20
Caatinga	CA-UNC	0.27	9.03	0.21	0.00	28.13	8.68	9.13	0.00	0.00	1.00
Amazonia	AM-COV	0.06	2.03	0.08	1.00	25.12	5.71	4.62	0.54	0.46	0.00
Amazonia	AM-COV	0.10	1.18	0.08	1.00	24.37	4.00	6.46	0.13	0.60	0.26
Amazonia	AM-COV	0.22	2.40	0.26	1.00	24.68	3.93	4.91	0.00	0.89	0.11
Amazonia	AM-COV	0.06	2.80	0.08	1.00	24.42	3.75	3.31	0.61	0.03	0.34
Amazonia	AM-COV	0.08	1.47	0.05	1.00	25.13	4.62	3.78	0.84	0.06	0.09
Amazonia	AM-COV	0.03	1.26	0.09	1.00	23.62	5.01	5.79	0.81	0.19	0.00
Amazonia	AM-COV	0.23	2.95	0.05	1.00	24.46	4.13	4.25	0.83	0.16	0.00
Amazonia	AM-COV	0.21	1.56	0.04	1.00	24.47	4.60	2.77	0.91	0.08	0.00
Amazonia	AM-COV	0.08	3.16	0.06	1.00	23.59	4.80	4.91	0.55	0.4	0.05
Amazonia	AM-COV	0.05	1.97	0.06	1.00	24.9	5.33	3.86	0.47	0.33	0.19
Amazonia	AM-COV	0.03	0.80	0.06	1.00	24.13	3.67	2.39	0.53	0.46	0.00
Amazonia	AM-COV	0.10	1.70	0.13	1.00	24.31	4.21	2.42	0.43	0.21	0.34
Amazonia	AM-COV	0.16	1.30	0.03	1.00	24.65	3.20	3.41	0.58	0.25	0.16
Amazonia	AM-UNC	0.12	4.33	0.21	0.00	28.2	5.84	4.70	0.00	0.34	0.65
Amazonia	AM-UNC	0.24	4.49	0.59	0.00	24.65	4.31	5.65	0.01	0.76	0.21
Amazonia	AM-UNC	0.23	7.22	0.41	0.00	25.60	4.64	4.40	0.00	0.41	0.58
Amazonia	AM-UNC	0.27	4.50	0.75	0.00	26.40	5.64	2.44	0.00	0.81	0.19
Amazonia	AM-UNC	0.23	5.71	0.30	0.00	26.90	6.02	3.47	0.00	0.20	0.79
Amazonia	AM-UNC	0.08	12.35	0.19	0.00	27.20	5.80	2.60	0.00	0.70	0.29
Amazonia	AM-UNC	0.29	5.31	0.22	0.00	24.98	4.67	4.98	0.04	0.89	0.06
Amazonia	AM-UNC	0.50	4.41	0.43	0.00	25.40	3.80	7.52	0.22	0.45	0.32
Amazonia	AM-UNC	0.22	4.84	0.50	0.00	24.10	4.99	4.90	0.00	0.83	0.16
Amazonia	AM-UNC	0.09	10.89	0.25	0.00	24.20	5.18	4.01	0.00	0.19	0.80
Amazonia	AM-UNC	0.96	8.13	0.58	0.00	26.40	4.93	3.52	0.00	0.98	0.01
Amazonia	AM-UNC	0.22	12.92	0.41	0.00	25.06	4.30	5.70	0.03	0.93	0.02
Amazonia	AM-UNC	0.12	9.84	0.31	0.00	25.20	4.94	6.11	0.02	0.55	0.42

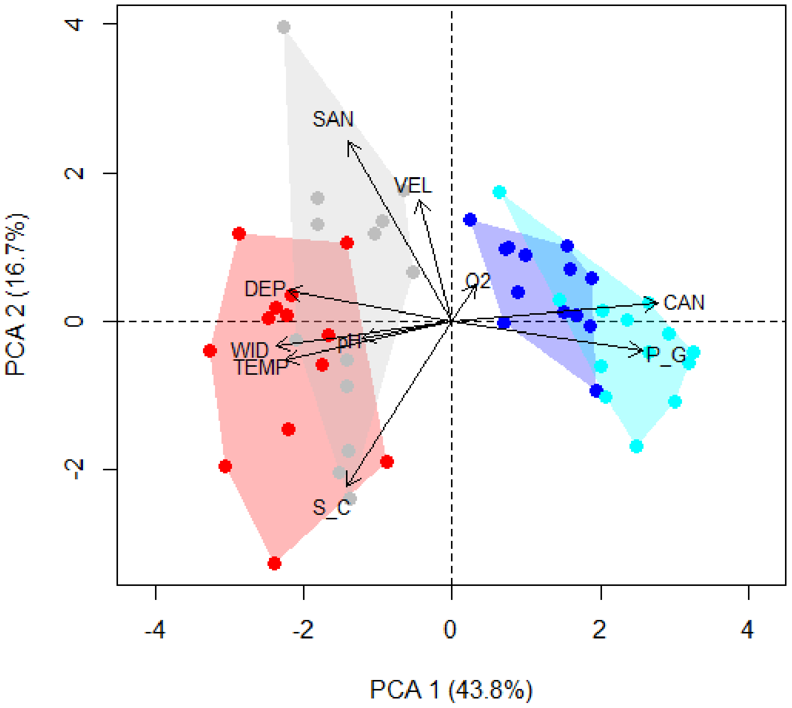

Figure A1.1 Final PCA graphics of streams selected in each biome. (blue) CA-COV; (cyan) AM-COV; (red) CA-UNC; (gray) AM-UNC.

Figure A1.2 Environmental structure of the streams sampled with rocky bottom characteristics, a high proportion of canopy cover and low depth, for the groups CA-COV (a) and AM-COV (b) and streams with sandy bottom characteristics and a low proportion of canopy cover for the CA-UNC (c) and AM-UNC (d) groups.

Appendix S2 Functional trait assessment

From the ecomorphological analysis, we obtained 15 functional traits (Table A2.1) related to the locomotion capacity, feeding acquisition and water column position in 122 species, similar to Leitão et al. 2016.

Table A2.1 List of 15 functional indexes measured from the ecomorphological traits of the species. 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 *et al.*, 2010
Pectoral-fin position	$\frac{PFi}{PFb}$	PFps	Pectoral fin use for maneuverability	Dumay *et al.*, (2004)
Aspect ratio of the pectoral fin	$\frac{PFl^2}{PFs}$	FPar	Pectoral fin use for propulsion	Adapted from Fulton *et al.*, (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 *et al.*, 2010
Fins surface to body size ratio	$\frac{(2*PFs)+CFs}{\frac{\pi}{4}*Bw*Bd}$	Fsf	Acceleration and/or maneuverability efficiency	Villéger *et al.*, 2010
Body mass	$\log(Massa+1)$	LogM	Metabolism, endurance and swimming abilit	Villéger *et al.*, 2010

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Appendix S3 Supplementary information related to multifunctional space.

Table A3.1 Eigenvalues, percentages of variance explained and quality of functional space by each axis.

	PC 1	PC 2	PC 3	PC 4
Eigenvalues	2.00	1.51	1.38	1.29
Percentage of variance	26.86	15.40	12.83	11.20
Cumulative percentage of variance	26.86	42.22	55.08	66.29
Quality of functional space	0.0057	0.0037	0.0018	0.0008

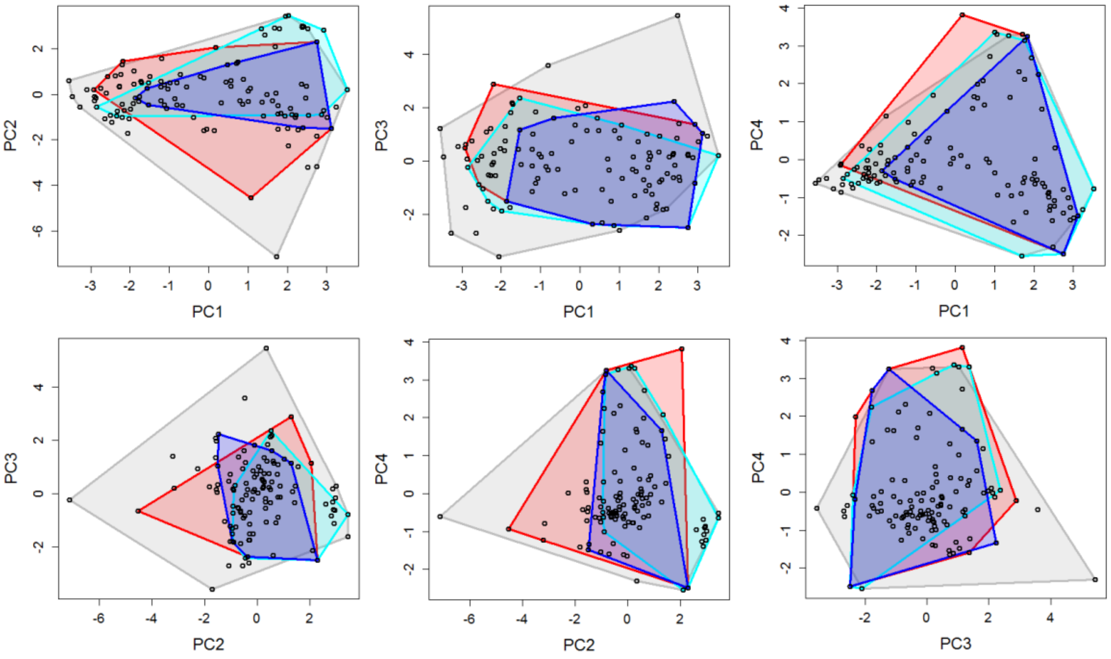

Figure A3.1 Four-dimensional functional space of the regional pool. (blue) CA-COV; (cyan) AM-COV; (red) CA-UNC; (gray) AM-UNC. Lines representing the convex hulls volumes of each stream group.

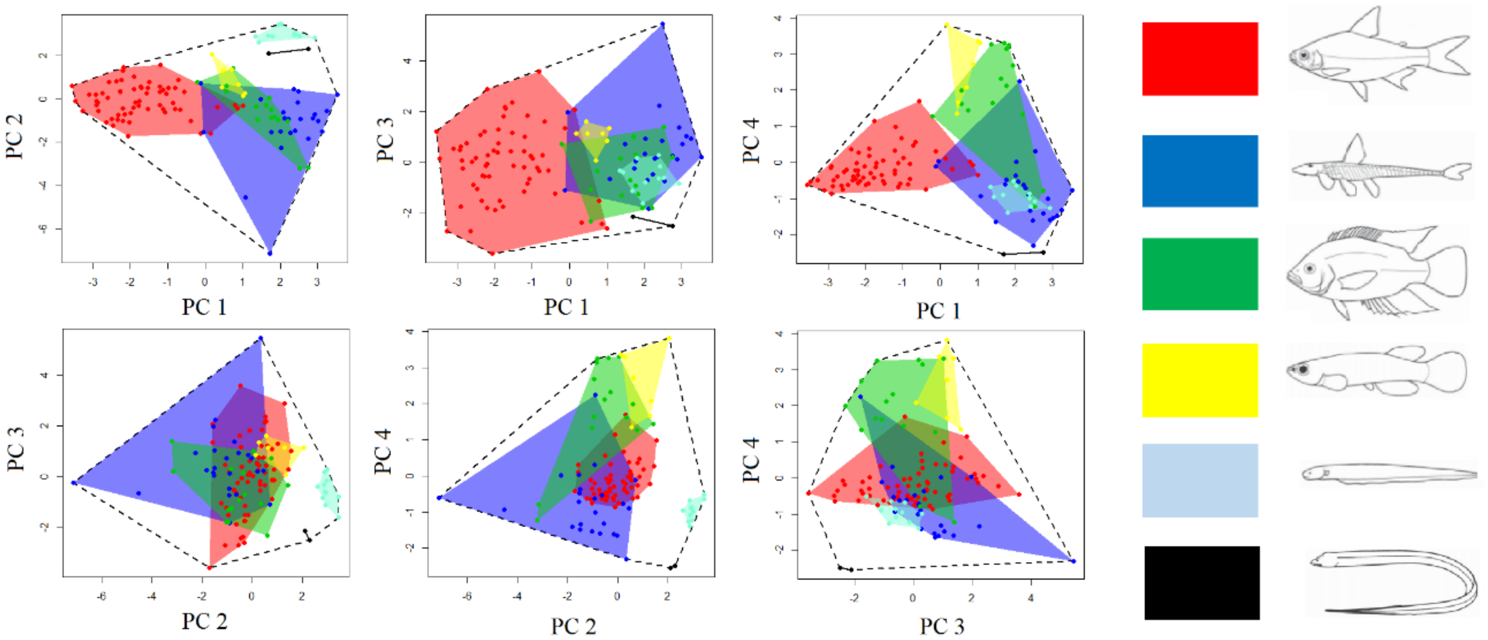

Figure A3.2 Functional space filled in four-dimensional of each order. (red) Characiformes; (blue) Siluriformes; (green) Perciformes; (yellow) Cyprinodontiformes; (aquamarine) Gymnotiformes; (black) Synbranchiformes.