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Heterogeneidade ambiental e diversidade de peixes de riachos na Amazônia

Belém, 2017

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Tese apresentada ao Programa de Pós-graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do título de Doutor em Zoologia.
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Orientadora: Profª. Drª. Maria Cristina Esposito
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Para Douglas

In all things of nature there is something of the marvelous

Aristóteles

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SUMÁRIO

Environmental heterogeneity and fish diversity of Amazon streams

ABSTRACT

Amazon streams are highly heterogeneous systems that encompass a remarkable diversity. Due to the increasing threats to these systems, it is necessary to understand how ecological process in natural areas affect streams and their fish biota. This thesis was divided in three chapters and aims to answer the following questions: 1) How much do catchment variables affect the physical habitat of small streams in the Amazon? 2) What is the relative contribution of environmental and spatial variables on taxonomic and functional alpha and beta diversity of stream fish? 3) How much are distinct components of biodiversity (species diversity, taxonomic distinctness, and functional diversity) congruent and how much can they be predicted from catchment variables? Fifty seven streams were sampled across six river basins in the Amazon region. For environmental characterization, a standardized protocol was used to obtain more than 140 local variables, and 11 catchment variables were obtained from aerial images. Fish assemblages were sampled with hand nets during a six-hour period. Stream catchments were divided in two groups based on altitude and slope. These two variables influenced streams habitats, regulating flow velocity and the types and proportions of substrates. The taxonomic and functional patterns of fish assemblages were affected by environmental filters operating at the catchment scale. Nonetheless, variables at the local scale were particularly important to taxonomic and functional alpha diversity. Despite the significant role of environmental filters, limited dispersal was the main driver of variation in fish diversity, indicating a strong biogeographic factor. Finally, various components of diversity exhibited intermediate congruence, which suggests that no single component can describe patterns of fish diversity. In addition, catchment variables alone could not accurately predict diversity patterns, and therefore it is recommended that additional explanatory variables, including descriptors of local environmental conditions, are important to include in studies of stream fish diversity.

Keywords: hierarchical models; variation partitioning; dispersal limitation; functional diversity; taxonomic distinctness.

Heterogeneidade ambiental e diversidade de peixes de riachos na Amazônia

RESUMO

Os riachos amazônicos são sistemas altamente heterogêneos e que abrigam uma enorme biodiversidade. Devido às crescentes ameaças a esses sistemas, aumenta-se a necessidade de entender como processos ecológicos em áreas naturais afetam os riachos e suas assembleias de peixes. Esta tese foi dividida em três capítulos e busca responder as seguintes questões: 1) O quanto das variáveis em escala de bacia regulam o hábitat físico de riachos amazônicos? 2) Qual a contribuição relativa do ambiente e do espaço sobre a diversidade alfa e beta, tanto taxonômica quanto funcional, de peixes de riachos? 3) O quanto diferentes componentes da biodiversidade (diversidade de espécies, distinção taxonômica e diversidade funcional) são congruentes e o quanto eles podem ser preditos a partir de variáveis em escala de bacia? Para responder estas questões, foram amostrados 57 riachos em seis bacias da região amazônica. Para a caracterização ambiental, foi aplicado um extenso protocolo padronizado, que gerou mais de 140 métricas locais, além da utilização de 11 variáveis em escala de bacia. As assembleias de peixes foram coletadas com redes de mão durante seis horas. Com os resultados, detectou-se que as bacias podem ser divididas em dois grupos a partir da altitude e declividade. Estas duas variáveis influenciaram os hábitats dos riachos, controlando a velocidade do fluxo e o tipo e proporção de substrato. Este controle foi fundamental para os padrões taxonômicos e funcionais das assembleias de peixes, que são afetadas pelo filtro ambiental na escala da bacia. Entretanto, variáveis locais foram particularmente importantes para a diversidade alfa, tanto taxonômica quanto funcional das espécies. Apesar do papel significativo dos filtros ambientais, a dispersão limitada foi o principal fator responsável por mudanças em todos os níveis de diversidade de peixes, o que indica um forte fator biogeográfico. Por fim, os diferentes componentes da diversidade exibiram congruência intermediária, o que demonstra que eles são complementares e que não é possível resumir a diversidade de peixes a um único componente. Além disso, as variáveis na escala de bacia mostraram capacidade intermediária de prever padrões de diversidade, sendo recomendável utilizar outras métricas preditoras, como variáveis locais, em estudos de diversidade de peixes.

Palavras-chave: modelos hierárquicos; partição de variância; dispersão limitada; diversidade funcional; distinção taxonômica.

INTRODUÇÃO GERAL

INTRODUÇÃO

A Bacia Amazônica é a maior bacia hidrográfica do mundo, drenando uma área de mais de seis milhões de Km² (Barthem et al. 2004). A mesma é formada por inúmeros corpos d'água de tamanhos variados, com destaque para os ambientes lóticos (rios e riachos). Essa bacia abriga a maior diversidade de peixes de água doce do mundo, com aproximadamente 2.000 espécies conhecidas e com estimativas de mais 1.000 espécies a serem descritas (Lundberg et al. 2010). Apesar da grande importância e diversidade da Bacia Amazônica, a maioria dos estudos ainda foca nos grandes rios e dá pouca ênfase aos riachos, que formam a maior parte das redes hidrográficas (Junk et al. 2007). Estes são fundamentais para a heterogeneidade da paisagem e para a manutenção da biota, pois são uma importante fonte de água para organismos terrestres (Meyer et al. 2007) e sustentam aproximadamente metade das espécies conhecidas de peixes na Amazônia (Junk et al. 2007).

Uma das razões por trás da grande diversidade encontrada nos riachos é sua alta heterogeneidade ambiental, e esta deriva de mudanças na paisagem. Características do hábitat, como tipo e proporção de substratos, morfologia do canal e velocidade da água, são diretamente reguladas por variáveis na escala de bacia, tais como a declividade, altitude e uso de solo (Leal et al. 2016; Snelder and Biggs 2002). Esta dependência entre escalas levou Hynes (1975) a declarar que "o vale controla o riacho", o que levou pesquisadores a formular diversos modelos hierárquicos (p.ex. Frissell et al. 1986; Snelder and Biggs 2002) buscando interpretar a variabilidade natural dos riachos no contexto da bacia de drenagem. Em ambientes bem preservados, determinar a extensão em que variáveis em escala de bacia controlam fatores em escala local é útil para fins conservacionistas, pois pode fornecer informações importantes sobre as condições de referência de riachos (Stoddard et al. 2006; Thieme et al. 2007). Entretanto, os riachos amazônicos ainda carecem desse tipo de informação (Thieme et al. 2007). Com as crescentes ameaças à biodiversidade e aos ambientes naturais, é fundamental caracterizar os fatores envolvidos no controle da variabilidade natural dos riachos. A Amazônia, região que ainda mantém áreas extensamente conservadas, apresenta condições ideais para uma avaliação detalhada da heterogeneidade ambiental dos riachos e de seus efeitos na diversidade aquática, fornecendo informações essenciais para estratégias de conservação (Castello et al. 2013; Portocarrero-Aya and Cowx 2016).

Tal hierarquia entre os fatores físicos fez com que se buscasse desatrelar os efeitos de variáveis ambientais em diferentes escalas sobre a diversidade dos peixes de riachos (Sály et al. 2011; Sharma et al. 2011; Zbinden and Matthews 2017). Sabe-se que os peixes respondem a mudanças na largura e profundidade do canal, cobertura vegetal e substrato (Leitão et al. 2017; Mendonça et al. 2005; Pease et al. 2011). Porém, variáveis como o clima e a geologia são encarregados por formar as principais feições dentro das bacias, podendo ser as principais responsáveis por dissimilaridades nas assembleias de peixe ao se comparar diferentes redes de drenagem (Hoeinghaus et al. 2007; Paller et al. 2016). Além disso, a inclusão de variáveis espaciais pode fornecer pistas adicionais sobre os processos que controlam as assembleias aquáticas. A autocorrelação espacial de variáveis ambientais faz com que riachos mais próximos sejam mais similares em seus fatores abióticos e, portanto, em seus conjuntos de espécies (Hoeinghaus et al. 2007). Além disso, o formato linear e dendrítico das redes de drenagem limita as possibilidades de dispersão e colonização de espécies obrigatoriamente aquáticas como os peixes (Sharma et al. 2011; Shurin et al. 2009). Esta dispersão limitada leva à maior similaridade entre riachos dentro da mesma bacia, e está diretamente associada a fatores históricos e biogeográficos (Reyjol et al. 2007; Sharma et al. 2011).

A influência da dispersão limitada e dos filtros ambientais têm sido avaliadas como potenciais processos que causam dissimilaridade nas assembleias de peixes de riachos, mas estudos recentes mostram que a diversidade funcional de peixes pode apresentar respostas distintas de sua contraparte taxonômica (Cilleros et al. 2016; Hoeinghaus et al. 2007). A diversidade funcional é definida como o valor e abrangência de atributos funcionais que influenciam o funcionamento do ecossistema (Tilman 2001), podendo ser mais sensível aos filtros ambientais que a diversidade taxonômica, já que a diversidade funcional é um reflexo da adaptação das espécies às condições locais (Díaz and Cabido 2001; Villéger et al. 2010). Assim, fica claro que o estudo da diversidade funcional fornece informações complementares para a compreensão dos fatores que controlam a distribuição das espécies.

Nas últimas décadas, essa necessidade de informações complementares no estudo da biodiversidade ficou cada vez mais clara (Meynard et al. 2011; Pool et al. 2014). Durante muito tempo, buscou-se métricas relativamente simples para representar a diversidade de espécies para a avaliação de processos ecológicos, biogeográficos e estudos de conservação (Magurran and Queiroz 2010; Stirling and Wilsey 2001). A métrica mais comumente utilizada é a riqueza de espécies, por esta ser a mais intuitivamente lembrada ao se pensar no conceito de biodiversidade (Magurran and Queiroz 2010; Wilsey et al. 2005). Entretanto, os resultados de estudos que utilizaram apenas a riqueza de espécies são limitados, já que estes só avaliam um componente da biodiversidade (Wilsey et al. 2005). Assim, estudos recentes passaram a incorporar novas métricas relacionadas a outros componentes, como a diversidade funcional e a distinção taxonômica, esta última uma aproximação da diversidade filogenética. A distinção taxonômica considera a relação evolutiva entre as espécies

(Heino et al. 2007; Warwick and Clarke 1995) e pode indicar a capacidade de um sistema para gerar novas soluções evolutivas em respostas a mudanças ambientais (Meynard et al. 2011).

A relação entre diferentes componentes de diversidade pode ajudar na tomada de decisões conservacionistas ao informar se diferentes áreas possuem níveis distintos ou não de diversidade em relação diversas facetas (Pool et al. 2014). Além disso, é importante determinar se essas métricas respondem de maneira similar a variáveis de grande escala, mais facilmente obtidas que variáveis de hábitat físico (Heino et al. 2007; Heino et al. 2008). A congruência entre diferentes componentes da diversidade e uma forte previsibilidade em relação a métricas de grande escala tornariam as medidas conservacionistas muito mais simples, baratas e rápidas (Carvalho and Tejerina-Garro 2015b; Heino et al. 2008).

Considerando o exposto acima, os objetivos gerais desta tese são avaliar o quanto variáveis do hábitat físico de riachos são reguladas por variáveis em escala de bacia e como variáveis ambientais e espaciais afetam as assembleias de peixes na Amazônia. Estes objetivos foram avaliados utilizando 57 riachos em bom estado de conservação distribuídos em seis bacias na Amazônia. Este trabalho foi dividido em três capítulos para investigar detalhadamente os objetivos gerais.

No primeiro capítulo, intitulado "*Regional controls on physical habitat structure of Amazon streams*", buscou-se determinar a relação entre diversas métricas do hábitat físico e métricas na escala de bacia. A hipótese testada é a de que as variáveis da bacia controlam fortemente as características do hábitat.

No segundo capítulo, intitulado "*Partitioning taxonomic and functional diversity of Amazon stream fish between environment and space*", o objetivo foi determinar o papel de variáveis espaciais e ambientais (divididas entre locais e de bacia) na diversidade alfa e beta taxonômica e funcional de peixes. Testou-se a hipótese que a diversidade alfa e beta taxonômica são mais afetadas elas variáveis de bacia, enquanto a diversidade alfa e beta funcionais são mais afetadas por variáveis do hábitat.

O terceiro capítulo, intitulado "*Are the patterns of different components of stream fish diversity congruent?*", teve como objetivo determinar a congruência nos padrões de três componentes de diversidade (diversidade de espécies, distinção taxonômica e diversidade funcional), bem como sua resposta à variáveis em escala de bacia. Espera-se que os três componentes respondam fortemente às variáveis da bacia.

MATERIAL E MÉTODOS

Área de estudo

Foram amostrados 57 riachos durante o período de seca entre 2012 e 2015. Estes riachos encontram-se distribuídos em seis bacias (Figura 1): Bacias dos rios Juruena (10 riachos amostrados), Negro (10), Anapu (10), Tapajós (7), Acará (10) e Capim (10). Os riachos das bacias do Juruena, Negro, Anapu, Tapajós estão localizados dentro de unidades de conservação, já os riachos das Bacias do Acará e do Capim estão em fragmentos florestais protegidos em áreas particulares.

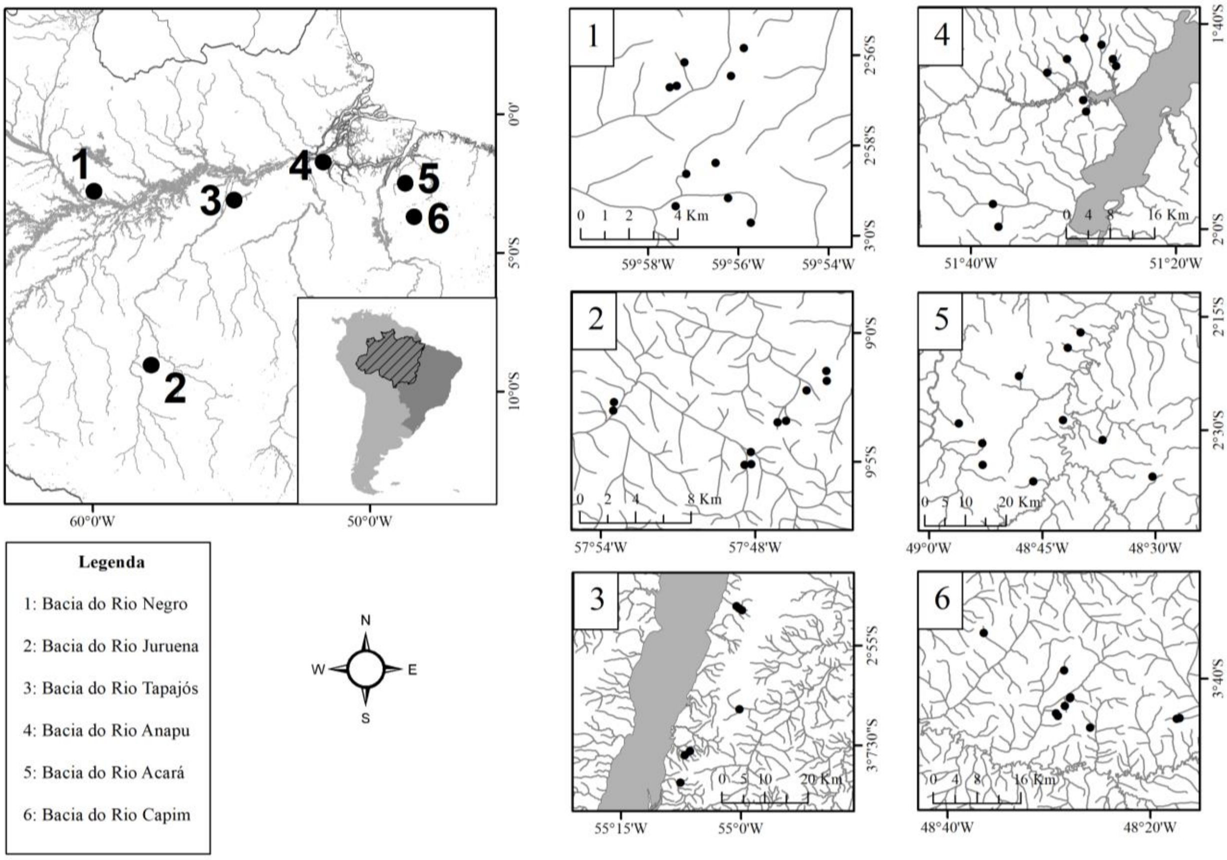

Figura 1. Localização das seis bacias de estudo amostradas na Amazônia. Foram amostrados 57 riachos nos períodos de seca de 2012 a 2015.

Bacia do rio Juruena

Todos os pontos coletados na bacia do rio Juruena (Figura 2A) estão localizados no Parque Nacional do Juruena, que ocupa uma área de 1.958.203 ha nos municípios de Apiacás, Nova Bandeirantes, Contriguaçu e Colniza, no Estado do Mato Grosso, Maués e Apuí, no Estado do Amazonas, e Jacareacanga, no Estado do Pará. O PARNA Juruena é coberto em mais de 50% por Floresta Ombrófila Densa e Aberta. O clima local é do tipo "Am" na classificação de Köppen, definido como tropical quente e úmido, com curto período de seca e sazonalidade bem definida (Peel et al. 2007). A temperatura média é de 25,7 °C, com máxima de 32 °C e mínima de 15 °C. A pluviosidade média anual varia de 2.000 a 2.500 mm, com período chuvoso de outubro a abril (350 mm) e período de estiagem de junho a setembro (10 mm) (ICMBio 2011).

Bacia do rio Negro

Os riachos amostrados nessa região (Figura 2B) encontram-se na Reserva Florestal Adolpho Ducke. A reserva, localizada próximo da cidade de Manaus, ocupa uma área de 10.000 ha coberta principalmente por floresta de terra firme. O clima é do tipo “Am” na classificação de Köppen (Peel et al. 2007), com temperatura anual média de 26,7 °C. A precipitação média é de 2.286 mm por ano, com período chuvoso se estendendo de novembro a maio e o seco, de junho a outubro (Mendonça et al. 2005).

Bacia do rio Tapajós

Todos os riachos amostrados na bacia do rio Tapajós (Figura 2C) foram amostrados na Floresta Nacional do Tapajós. A reserva, que ocupa quase 545 mil ha, está localizada nos municípios de Belterra, Aveiro, Placas e Rurópolis, no Estado do Pará. A vegetação do tipo Floresta Ombrófila Densa cobre mais de 85% do território da FLONA. O clima é do tipo Am na classificação de Köppen. A temperatura média anual é de 25,5 ºC, com mínima de 21 ºC e máxima de 30,6 ºC. A precipitação média anual é de 1.820 mm, com o período chuvoso se estendendo de janeiro a maio e o seco, de junho a dezembro (IBAMA 2004).

Bacia do rio Anapu

Todos os riachos amostrados na bacia do rio Anapu (Figura 2D) estão localizados na Floresta Nacional de Caxiuanã, nos municípios de Portel e Melgaço, Estado do Pará. A FLONA de Caxiuanã possui 85% de sua área coberta por Floresta Ombrófila Densa de Terra Firme. O clima local é do tipo “Am” na classificação de Köppen. A temperatura média é de 26,7 ºC, com mínima de 23 ºC e máxima de 32,7 ºC. A pluviosidade média anual alcança 2.000 mm, com a maior incidência de chuvas no mês de março (379 mm) e a menor, em outubro (50 mm) (Lisboa 2002). O sistema hidrográfico de Caxiuanã apresenta características predominantemente lacustres, pois constitui um “lago de ria” derivado do afogamento de vales do rio Anapu durante o Holoceno (Behling and Costa 2000). Como resultado, os riachos possuem baixa velocidade de correnteza, um canal principal associado com uma extensa planície de inundação e o leito densamente recoberto por serapilheira (Montag et al. 2009).

Bacia do rio Acará

Os riachos amostrados na bacia do rio Acará (Figura 2E) estão localizados na área da empresa Agropalma, nos municípios de Tailândia, Tomé-Açu, Acará e Moju. A empresa possui oito fragmentos florestais que somam 50.000 ha, sendo que 90% desse montante são de Floresta Ombrófila Densa de Terra Firme. O clima local é do tipo "Af", caracterizado como equatorial úmido (Peel et al. 2007). A pluviosidade média é de 2.344 mm, com ápice do período de chuvas em março (427 mm) e ápice do período de estiagem em setembro (54 mm) (Albuquerque et al. 2010). A temperatura média é de 26 °C (Luiza-Andrade et al. 2017).

Bacia do rio Capim

Os riachos amostrados nessa bacia (Figura 2F) estão localizados dentro da área da empresa Cikel Ltda. A região é coberta, em sua maior parte, por Floresta Ombrófila Densa Submontana (Prudente et al. 2017). O clima é do tipo "Af" na classificação de Köppen (Peel et al. 2007). A temperatura média anual é de 27,2 ºC. A precipitação média anual é de 1.765 mm, com um período de estiagem ocorrendo entre os meses de julho a novembro (Watrin and Rocha 1991).

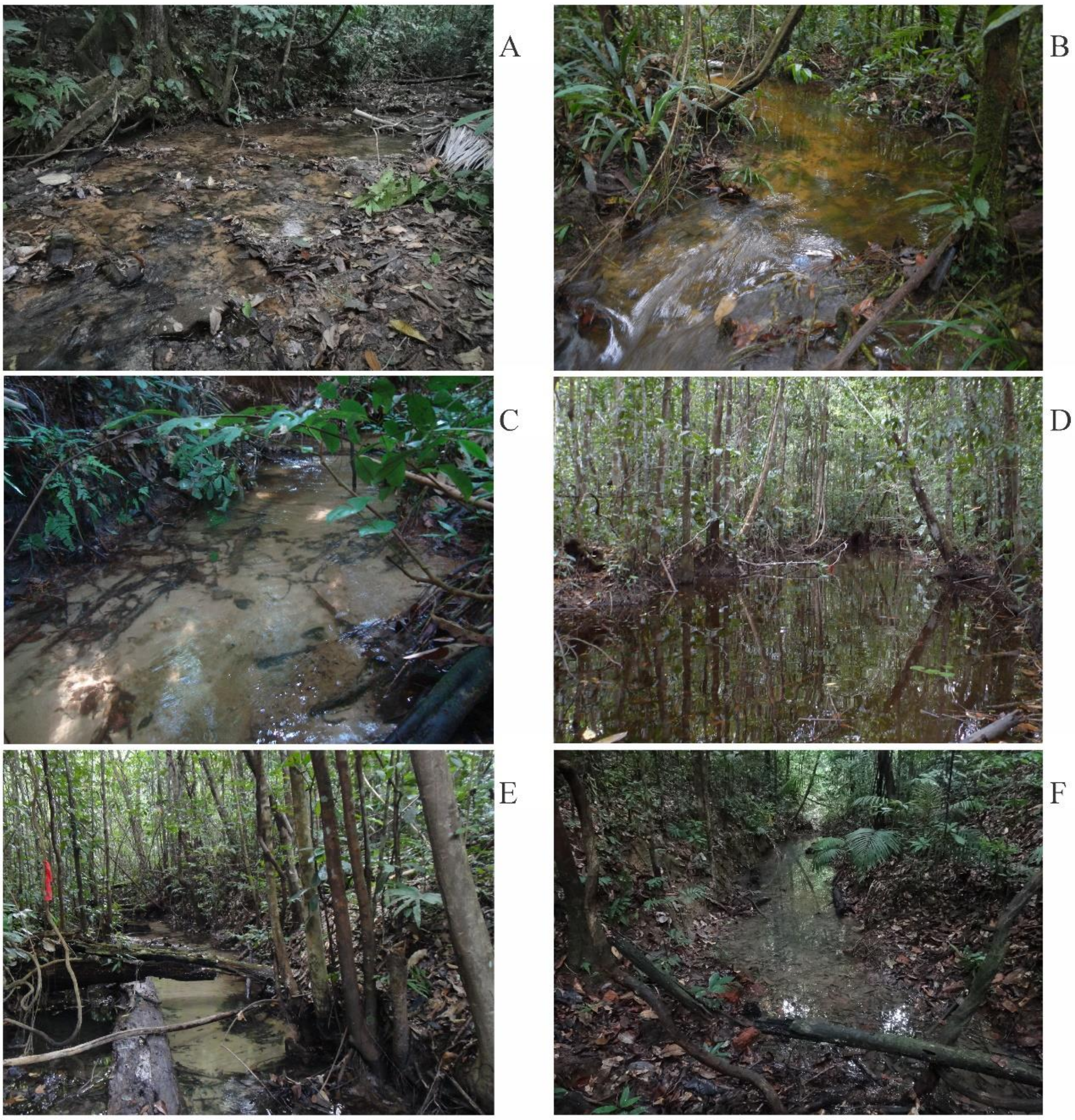

Figura 2. Exemplo de riachos amostrados nas bacias dos rios Juruena (A), Negro (B), Tapajós (C), Anapu (D), Acará (E) e Capim (F) entre os anos de 2012 e 2015.

Delineamento amostral

Em cada riacho, foi demarcado um trecho de 150m que foi dividido em 10 segmentos de 15m, totalizando 11 transecções e 10 seções longitudinais. As transecções foram nomeadas de A a K, enquanto as seções foram nomeadas a partir da combinação dos nomes das transecções limitantes (A-B, B-C, C-D, ..., J-K) (Figura 3).

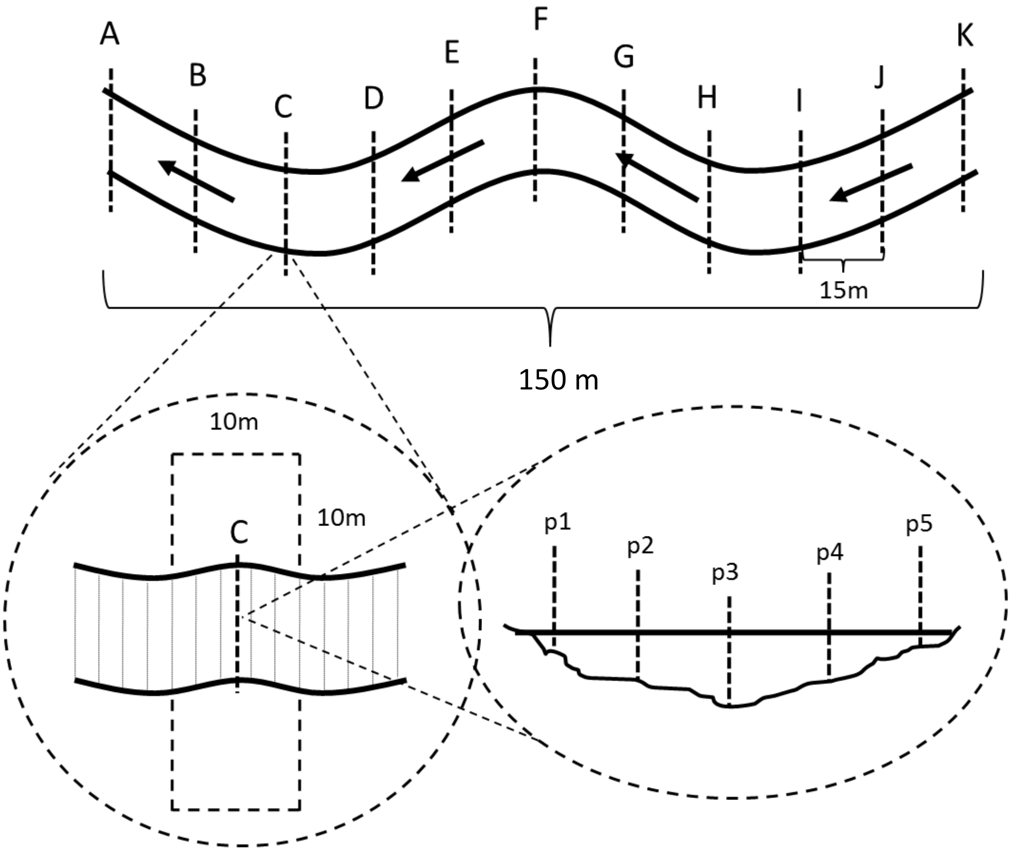

Figura 3. Esquema do trecho de riacho. As letras (A-K) indicam as transecções, marcadas a cada 15m. As seções longitudinais se referem aos segmentos entre as transecções.

Coleta de variáveis locais

Para mensuração das variáveis estruturais do ambiente, foi aplicada uma versão modificada (Callisto et al. 2014) do Protocolo de Avaliação e Monitoramento Ambiental (US-EPA) descrito por Kaufmann et al. (1999) e Peck et al. (2006). Originalmente, este protocolo visa avaliar as condições físicas em que os riachos se encontram, considerando as mudanças antrópicas afetando os corpos d’água. Entretanto, como o presente estudo foi aplicado apenas em riachos bem conservados, o mesmo foi utilizado apenas como protocolo de caracterização do hábitat físico.

Nas transecções, foram tomadas as seguintes variáveis:

1) **Largura molhada (m):** largura do canal, medida através de fita métrica.
2) **Profundidade do canal (cm):** medida com o uso de um cano graduado em cinco pontos equidistantes
3) **Tipo de substrato e imersão:** tomado nos mesmos cinco pontos da profundidade do canal. A classificação é feita em categorias (ex: areia, silte, banco de folhas, cascalho grosso)

determinadas a partir do tamanho do sedimento (Figura 4). A imersão do substrato no sedimento fino é estimada visualmente.

Figura 4. Diferentes substratos encontrados nos leitos dos riachos amostrados na Bacia Amazônica.

4) **Cobertura de dossel:** mensurado em seis pontos (direita, centro direita, centro montante, centro jusante, centro esquerda e esquerda) com o uso de densiômetro (Figura 5).

Figura 5. Uso do densiômetro para medição da cobertura de dossel dos riachos amostrados na Bacia Amazônica.

5) **Abrigo para peixes:** estimativa visual de alguns componentes estruturais do riacho, como banco de folhas, algas filamentosas e matacões. Essa estimativa é feita considerando os 5 m anteriores e posteriores à transecção, cobrindo uma extensão de 10 m.
6) **Zona ripária:** estimativa visual da cobertura proporcionada pela zona ripária em ambas as margens. Inclui desde árvores de grande porte até plantas rasteiras e solo nu. Essa estimativa é feita considerando os 5 m anteriores e posteriores à transecção, e uma extensão de 10 m a partir de cada margem, formando plots de 100 m^2.

Nas seções longitudinais, foram tomadas as seguintes variáveis em 15 pontos equidistantes:

1) **Profundidade do talvegue (cm):** medido com o uso de um cano graduado.
2) **Tipo de unidade do hábitat do canal:** determinada a partir do tipo principal de classe de hábitat do canal em uma linha transversal (Figura 6). A unidade do canal varia de fluxo suave até cascata e queda d'água, podendo haver formação de vários tipos de piscina.

Figura 6. Exemplo de alternância de unidades de canal nos riachos das seis áreas amostradas na Bacia Amazônica. 1 = Fluxo suave; 2 = Rápido.

3) **Largura molhada:** medidas no 1º e 8º pontos da seção longitudinal.
4) **Tipo de substrato:** medido em cinco pontos transversais equidistantes no 8º ponto da seção longitudinal.
5) **Presença de pedaços grandes de madeira:** foram contados tanto os que estão imersos na água quanto os que estão suspensos sobre o canal. Os pedaços de madeira foram registrados a partir de categorias de tamanho que incluem o volume ocupado pela madeira.

6) **Declividade do canal:** determinada com o uso de uma mangueira e duas réguas.
7) **Velocidade da água (medida uma única vez):** mensurada através do método do objeto flutuante.

Essas variáveis foram combinadas para formar novas variáveis seguindo o descrito por Kaufmann et al. (1999). Em cada capítulo, há tabelas nos materiais suplementares com o resumo estatístico das métricas utilizadas.

Variáveis de bacia

Foram utilizadas 11 variáveis como características das bacias de drenagem a montante de cada sítio amostral: temperatura média anual (ºC), temperatura do trimestre mais seco (ºC), precipitação média anual (mm), precipitação do trimestre mais seco (mm), altitude (m), declividade da bacia (%), área drenada (Km²) e proporção de fragmentos grandes (> 2 mm, %), argila (%), areia (%) e silte (%) no solo.

As variáveis climáticas foram obtidas pelo BioClim (http://www.worldclim.org/bioclim). A altitude, declividade e área drenada foram calculadas com a ferramenta ArcHydro no software ArcGIS a partir de imagens de satélite (*Shuttle Radar Topography Mission* – SRTM) com 30 m de altitude, obtidas no site EarthExplorer (http://earthexplorer.usgs.gov/). Os dados de solo, todos com profundidade de 0 cm, foram obtidos no site SoilsGrid1km (http://soilgrids1km.isric.org/). A proporção de cada variável de solo foi calculada utilizando a ferramenta *Spatial Analyst tool* no software ArcGis.

Coleta de peixes

Os peixes foram coletados com redes de mão (Figura 7) de 55 cm de diâmetro e malha de 2 mm durante um período de 6h, sendo este tempo dividido entre dois ou três coletores. Os peixes foram mortos com doses letais de anestésico (Leary et al. 2013), fixados em formalina 10% durante 72h, e foram posteriormente conservados em álcool 70%. Os exemplares foram identificados ao nível taxonômico mais apurado possível através de literatura especializada e consulta a especialistas. Os mesmos serão depositados na Coleção Ictiológica do Museu Paraense Emílio Goeldi.

Figura 7. Exemplo de coleta de peixes utilizando rede mão nos riachos amostrados na Bacia Amazônica.

Dados funcionais

Foram obtidos *traits* funcionais de cinco indivíduos de tamanho similar de cada espécie. Para espécies com dimorfismo sexual, foram selecionados apenas indivíduos do sexo feminino (Ribeiro et al. 2016). *Traits* quantitativos foram obtidos a partir de 16 medidas morfológicas: comprimento padrão (CP), altura máxima do corpo (AMC), largura máxima do corpo (LMC), comprimento do pedúnculo caudal (CPC), altura máxima do pedúnculo caudal (APC), largura máxima do pedúnculo caudal (LPC), comprimento da nadadeira peitoral (CNP), altura máxima da nadadeira peitoral (AMNP), altura da linha média do corpo (ALMC), altura da linha média do olho (ALMO), comprimento da cabeça (CC), altura da cabeça (AC), largura da boca (LB), área do corpo (ADC), área da nadadeira peitoral (ANP) e orientação da boca (OB) (Ohlberger et al. 2006; Watson and Balon 1984).

Todas as medidas foram tomadas com o uso um paquímetro digital de 150 mm com precisão de 0,1 mm. As áreas das nadadeiras foram obtidas através do desenho do contorno das mesmas sobre papel manteiga, que foram posteriormente digitalizados e tratados no software ImageJ. As medidas foram utilizadas para calcular 12 índices ecomorfológicos (Ohlberger et al. 2006; Watson and Balon 1984) relacionados à posição vertical, locomoção e orientação (Tabela 1). Além disso, as espécies foram classificadas em grupos tróficos (carnívoros, hematófagos, invertívoros alóctones, invertívoros autóctones, invertívoros gerais, onívoros e perifitívoros) seguindo a literatura (p.ex. Brejão et al. 2013; Carvalho and Tejerina-Garro 2015a; Zuanon et al. 2015). Quando a informação não estava disponível para a espécie, os dados foram extrapolados a partir do gênero ou da família.

Tabela 1. *Traits* funcionais quantitativos analisados em peixes de riachos amostrados na Bacia Amazônica (Ohlberger et al. 2006; Watson and Balon 1984).

Característica	Fórmula	Explicação
Índice de compressão	IC = AMC/LMC	Altos valores indicam espécies comprimidas que habitam ambientes lênticos
Altura relativa do corpo	AR = AMC/CP	Valores menores indicariam peixes que habitam águas rápidas
Comprimento relativo do pedúnculo caudal	CRP = CPC/CP	Altos valores estão associados a maior capacidade de natação
Índice de compressão do pedúnculo caudal	ICP = APC/LPC	Valores elevados indicam pedúnculos comprimidos, associados a nadadores pouco ativos
Índice de aplanamento ventral	IAV = ALMC/AMC	Valores menores indicam peixes hidrodinâmicos, que mantém sua posição espacial inclusive parados
Área relativa da nadadeira peitoral	ARP = ANP/ADC	Valores altos indicam nadadores lentos que realizam manobras com as nadadeiras peitorais, ou peixes que de águas turbulentas que precisam ficar aderidos ao substrato
Aspecto proporcional da nadadeira peitoral	RAP = CNP/AMNP	Valores elevados indicam nadadeiras compridas, próprias para percorrer distâncias longas ou natação constante
Comprimento relativo da cabeça	CRC = CC/CP	Altos valores indicam consumo de presas grandes
Posição relativa dos olhos	PRO = ALMO/AC	Altos valores indicam olhos dorsais, encontrados normalmente em peixes bênticos
Largura relativa da boca	LRB = LB/CP	Altos valores indicam peixes que se alimentam de presas mais largas

Orientação da boca	OB	A orientação da boca indica em que parte do hábitat o peixe obtém seu alimento. Inferior = entre 10° e 80°; Terminal = 90°; Superior = entre 100° e 170°; Ventral= 0°. Os valores em graus foram convertidos em radianos (unidade de ângulo plano), para permitir a comparação com atributos com unidades de outra natureza, mas com a mesma dimensão
Coeficiente de finura	$CF = CP/\sqrt{(AMC * LMC)}$	Avalia a influência da forma do corpo sobre a capacidade de natação. Valores de 2 a 6 indicam arraste reduzido; a relação ótima para o nado eficiente é 4,5

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Capítulo 1

Regional controls on physical habitat structure of Amazon streams

O capítulo I desta tese foi elaborado e formatado conforme as normas da publicação científica *River Research and Applications*, as quais se encontram em anexo (Anexo 1)

Regional controls on physical habitat structure of Amazon streams

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ABSTRACT

Drainage basins are inherently hierarchical and are comprised of a series of nested subsystems, in which the functions and structure of lower levels depend on the features of higher levels. For a comprehensive understanding of the functioning of river systems, it is necessary to identify which factors are important at different scales and how they interact. Considering the importance of assessing lotic systems in the Amazon, our aim was to answer the following question: how do regional features at catchment scale constrain local physical habitat of streams? We sampled 55 streams distributed among six protected river basins of the Amazon, examining the associations of 11 catchment metrics with 146 local variables describing physical habitat structure derived from field measurements. Multivariate analyses showed that basins were structured according to different factors at both scales; variables related to substrate, cover for aquatic organisms, and fast channel habitats were explained by altitude, catchment slope, and proportion of coarse fragments in soils.

Altitude was the most important catchment variable, strongly affecting flow velocity and regulating channel morphology and sediment transport. Spatial differences in environmental heterogeneity indicate that different processes act at each scale; this emphasizes how difficult it is to choose the most relevant spatial scale in ecological studies. Our results highlight the importance of regional variables, especially altitude and slope, as drivers of local-scale environmental heterogeneity. We hope these results will help in developing more efficient monitoring projects and restoration practices to better understand and conserve aquatic resources in the Amazon Basin.

Key words: physical habitat structure; aquatic ecosystems; environmental heterogeneity; protected areas; fluvial hierarchy.

INTRODUCTION

Streams are highly heterogeneous ecosystems, and their configurations are primarily determined by regional factors at catchment scale, such as climate, geology, and land cover (Vannote *et al.*, 1980; Frissell *et al.*, 1986; Snelder and Biggs, 2002). The links between local physical habitat and regional features of drainage basins have led to the development of several hierarchical models, which define drainage basins as a series of nested subsystems, where the functions and structure of lower levels depend on the features of higher levels (Hynes, 1975; Frissell *et al.*, 1986; Snelder and Biggs, 2002).

For a comprehensive understanding of the functioning of streams and rivers systems, it is necessary to identify which factors are important at each scale and how they interact (Vannote *et al.*, 1980; Frissell *et al.*, 1986; Snelder and Biggs, 2002; Grabowski *et al.*, 2014). This knowledge can provide information for several ecological processes and conservation efforts. For example, differences in environmental filters at local and regional scales are responsible for variation in diversity patterns and aquatic community compositions; therefore, detecting key variables helps to determine the relative importance of each scale to biotic patterns (Vannote *et al.*, 1980; Wang *et al.*, 2003). In streams assessment and management approaches, reference streams (preserved or less impaired) are usually compared to impaired streams to quantify anthropogenic impacts on biotic and abiotic stream components. However, natural variations at both scales must be considered when selecting and characterizing reference sites, so that they are properly contrasted against impaired streams (Hughes *et al.*, 1986; Grabowski *et al.*, 2014).

In the Amazon Basin, the huge network formed by streams is a key contribution to landscape heterogeneity; its importance lies on the fact that it is a source of water, it maintains aquatic biodiversity, and it supplies ecosystemic services (Barthem *et al.*, 2004; Junk *et al.*, 2007; Castello *et al.*, 2013). Despite their importance, Amazon streams are still poorly studied, and little is known on factors that regulate their variability (Junk *et al.*, 2007; Castello *et al.*, 2013). Since the Amazon still has large relatively preserved areas, a proper assessment would provide essential information to guide management strategies (Thieme *et al.*, 2007; Castello *et al.*, 2013; Portocarrero-Aya and Cowx, 2016), biodiversity assessment, and species distribution modelling (Frederico *et al.*, 2014; Fagundes *et al.*, 2016).

Considering the large size of the Amazon Basin, high structural variation is expected, but little is known about the factors that regulate such heterogeneity. High deforestation rates and land use changes over the last decades have been degrading streams at a much faster pace than scientists can study them (Chaves *et al.*, 2008; Castello *et al.*, 2013). Without basic knowledge about the structure and function of Amazon streams ecosystems, the development of methods capable of preventing or mitigating impacts is severely hampered (Bleich *et al.*, 2016; Leal *et al.*, 2016). Therefore, identifying associations between physical habitat in small streams of protected drainages and the natural environmental factors that likely control stream habitat will help to factor out natural variability and allow more accurate diagnosis of anthropogenic effects.

The use of regional variables at catchment scale as drivers of local physical habitat variability is useful to identify stream conditions in first assessments of remote areas, minimizing the need for expensive, time-consuming field surveys. Considering the importance of assessing stream conditions and heterogeneity in the Amazon, we aimed to answer the following question: How much is the local physical habitat of streams affected by regional features at catchment scale? Our hypothesis is that regional variables will be important drivers of local physical habitat due to the hierarchical nature of drainage systems.

MATERIAL AND METHODS

Study area

We sampled 55 streams distributed in six river basins (Figure 1): Juruena (10 streams), Negro (10), Anapu (10), Tapajós (7), Acará (8), and Capim (10) River Basins. All streams are in protected areas: the first four basins are situated in conservation units and the last two are in protected forested fragments of private areas. We aimed to capture the largest possible variability inside each basin.

The six river basins are distributed across the Amazon rainforest, and are primarily covered by Terra firme Dense Ombrophilous Forest (Barthem *et al.*, 2004). All studied river basins are below 400m of altitude, with the lowest elevations in Anapu Basin and the highest in Juruena Basin (Barthem *et al.*, 2004). Climate in Acará and Capim is type “Af”, described as tropical rainforest with a short dry period between September and November. Climate in the other basins is type “Am”, described as tropical with monsoons and longer dry periods (Peel *et al.*, 2007). Mean temperature is 25-27º C, with little variation over the year. Mean annual precipitation is 2000 mm (Barthem *et al.*, 2004). The Anapu River Basin stands out among the other basins for its lacustrine features derived from the drowned valleys of the river during the Holocene (ria lakes, Sioli, 1967; Behling and Costa, 2000). Thus, stream velocity is very low, the main channel is associated with extensive floodplains, and the streambed is covered by coarse litter (Montag *et al.*, 2009).

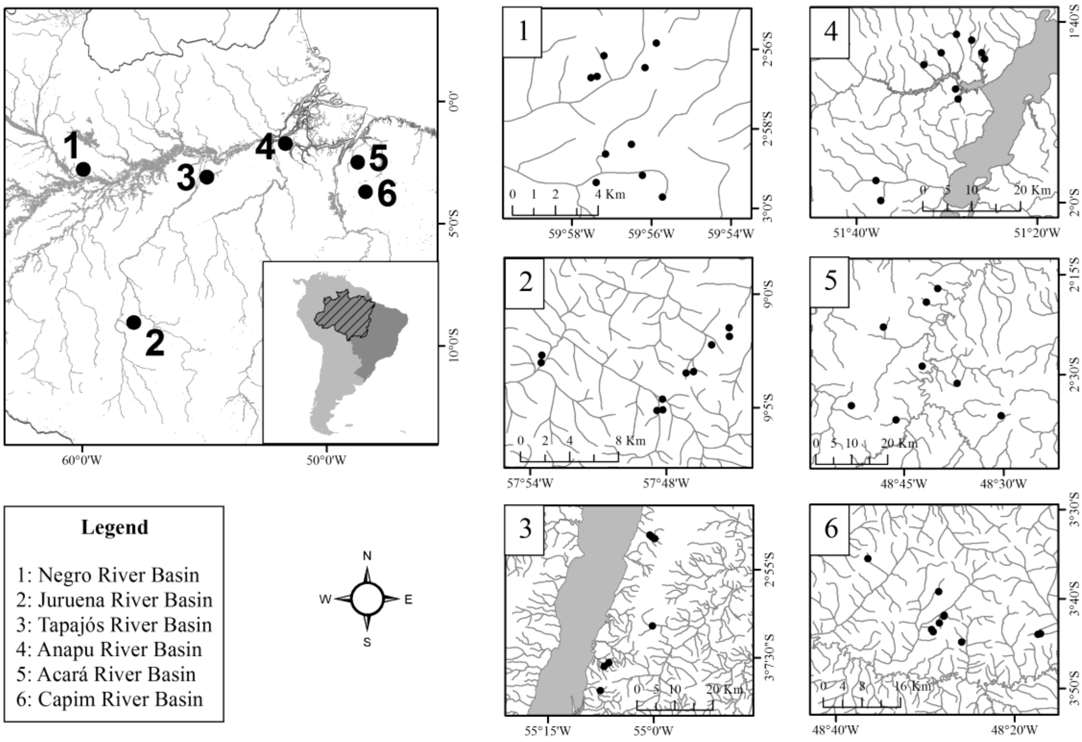

Figure 1. Location of the 55 sampled streams, distributed in six river basins of the Amazon.

Local physical habitat structure

In each stream, we sampled a 150-m reach, divided into ten 15-m longitudinal sections by 11 equidistant cross-sections. We applied a modified version (Callisto *et al.*, 2014) of the physical habitat assessment protocol of the U. S. Environmental Protection Agency (US-EMAP, Kaufmann *et al.*, 1999; Peck *et al.*, 2006), which resulted in 146 instream variables divided in six blocks: channel morphology (e.g. width, depth), substrate (e.g. bedrock, sand), channel habitat units (e.g. riffle, pool), riparian vegetation cover (e.g canopy cover, barren ground), large woody pieces (> 1,5 m long and > 10 cm at small end diameter), and instream cover for aquatic organisms (e.g. coarse and fine litter). All local physical metrics are listed in Table S1.

According to Peck *et al.* (2006), this protocol is more efficient under low flow conditions, which occur during dry season. Thus, all streams were sampled during that season.

Catchment-scale variables

We defined eleven catchment variables as the mean characteristics of the contributing drainage areas upstream of each sample site: mean annual air temperature (ºC), temperature of the driest quarter (ºC), mean annual precipitation (mm), precipitation of the driest quarter (mm), altitude (m), catchment slope (%), drainage area (km²), and proportion of coarse fragments (> 2 mm, %), clay (%), sand (%) and silt (%) in soil. Temperature and precipitation were obtained at BioClim (http://www.worldclim.org/bioclim). Using Shuttle Radar Topography Mission (SRTM) images, obtained at EarthExplorer (http://earthexplorer.usgs.gov/), we calculated altitude, catchment slope, and drainage area using the ArcHydro tool with ArcGis software. Soil data at 0 cm depth were obtained at SoilsGrid1km (http://soilgrids1km.isric.org/). We calculated the proportion for each soil variable using Spatial Analyst tool with ArcGis software. The complete list of catchment metrics can be found in Table S1. These variables were chosen for being well known natural drivers of local variation in small waterbodies (Frissell *et al.*, 1986; Snelder and Biggs, 2002; Grabowski *et al.*, 2014; Schneider *et al.*, 2015).

Data analysis

To reduce the number of local variables, we excluded metrics with low coefficient of variation (≤ 10 %) and variables with zero values at many (≥ 80%) sites. After that, all proportion variables were transformed (ln (x+1)) to improve data fitness to normal distribution. Other variables were z-score transformed to remove the effect of measures in different units (Legendre and Legendre, 2012). We used Pearson correlation coefficient to assess multicollinearity, excluding one correlated variable until all correlation pairs were ≤ 0.7. For each block with more than three remaining variables, we used Euclidean distance among streams and applied a Canonical Analysis of Principal Coordinates (CAP, Anderson and Willis, 2003), using the six basins as a categorical constrained factor to test whether there were differences between local characteristics of streams in distinct river basins. We selected only canonical axes with δ ≥ 0.6, as they had the strongest associations with the multivariate data cloud and the hypothesis of group differences (Anderson *et al.*, 2008), and retained metrics with loadings ≥ 0.6 on these axes. We assessed multicollinearity again with the retained variables. The same sequence of steps was followed using catchment metrics.

To characterize environmental conditions at both scales, we used the remaining local and catchment variables separately. We transformed all catchment variables using square root (coarse fragments) or log (all other variables) for better adjustment to normal distribution. We used two CAPs to visualize how streams were structured across different basins, examining variables at local and catchment scales separately, then retaining the most important variables (loadings ≥ 0.6 with axes δ ≥ 0.6). In order to test if the six studied basins were different, we applied a Permutational Analysis of

Multivariate Variance (PERMANOVA, Anderson, 2001), followed by a Permutational Analysis of Multivariate Dispersions (PERMDISP, Anderson, 2006) to detect if river basins had different levels of environmental heterogeneity. The higher the mean distance to group centroid, the higher the environmental heterogeneity.

Finally, we used multiple regressions with forward selection procedure to determine if local physical habitat variables were structured by catchment features, with the former as dependent variables and the latter as independent variables. In this case, data were not separated by river basins.

All analyses were run in R software (R Development Core Team, 2016) using vegan package (Oksanen *et al.*, 2016), with 4999 permutations and $\alpha = 0.05$.

RESULTS

After reduction of metrics, 15 physical habitat variables remained (Table 1). Nine were excluded for having low coefficients of variation, 26 for having too many zeroes, 76 were collinear with other variables, and 20 had low loadings on Canonical Analysis of Principal Coordinates (CAP) axes per block. Regarding catchment metrics, five variables had low coefficients of variation and one was collinear (precipitation of driest quarter with altitude = 0.70), and five variables remained (Table 1). Table S1 shows the summary of all local and catchment variables, along with each exclusion method. Table S2 shows all the matrices of correlation.

Table 1. List of remaining local and catchment metrics, with mean and standard deviation (SD) for each river basin. Size class 1 = woody pieces ≥ 0.3 m at small end diameter and ≥ 0.1 m length. Size class 4 = woody pieces ≥ 0.6 m at small end diameter and ≥ 15 m length.

Block of variables	**Variable name**	**Acará**	**Anapu**	**Capim**	**Negro**	**Juruena**	**Tapajós**
Channel morphology	SD thalweg depth (cm)	9.16 ± 3.83	11.35 ± 2.06	10.58 ± 2.72	13.92 ± 3.29	11.52 ± 5.88	2.59 ± 0.58
Substrate	Proportion of silt/muck/clay (%)	6.5 ± 3.73	26.1 ± 31.18	9.59 ± 6.97	0.67 ± 1.01	20.09 ± 9.44	10.8 ± 17
	Fine substrates (< 16 mm diameter) (fine gravel, sand and silt/muck/clay) (%)	37.17 ± 13.55	26.1 ± 31.18	37.76 ± 12.06	38.75 ± 11.62	54.98 ± 15.34	49.3 ± 11.37
	Proportion of wood (%)	6.50 ± 4.30	21.14 ± 8.18	5.10 ± 4.29	5.27 ± 2.17	4.70 ± 3.75	5.88 ± 2.52
	Proportion of roots and trees (%)	7.67 ± 4.98	6.86 ± 9.64	6.48 ± 4.70	36.57 ± 9.76	3.05 ± 4.51	22.36 ± 7.59
Channel habitat units	Proportion of rapids (%)	0.08 ± 0.24	0.00 ± 0.00	0.60 ± 0.58	3.67 ± 4.80	13.67 ± 20.97	10.98 ± 15.19
	Fast channel habitats (falls + cascade + rapids + riffles) (%)	34.61 ± 30.55	7.53 ± 22.45	23.80 ± 17.62	54.67 ± 18.10	64.20 ± 31.03	46.95 ± 29.44
Riparian vegetation cover	SD canopy at banks (%)	2.69 ± 1.35	3.62 ± 2.59	5.98 ± 4.62	4.87 ± 1.81	9.19 ± 6.03	4.39 ± 1.57
	SD barren ground (%)	1.22 ± 2.06	0.50 ± 1.32	2.21 ± 2.54	3.06 ± 4.88	2.41 ± 1.72	3.30 ± 4.64
	Total riparian cover (%)	200.5 ± 56.2	237.59 ± 34.21	180.35 ± 23.07	265.16 ± 41.55	242.52 ± 31.14	230.84 ± 24.86
Large woody pieces	Number of large woody pieces inside + above channel / m² - size class 1	0.22 ± 0.17	0.1 ± 0.05	0.12 ± 0.06	0.14 ± 0.05	0.07 ± 0.03	0.06 ± 0.03
	Volume of large woody pieces inside + above channel / m² - size class 4	0.05 ± 0.04	0.1 ± 0.17	0.01 ± 0.01	0.04 ± 0.07	0.06 ± 0.07	0 ± 0.01

Instream cover for aquatic organisms	Mean natural cover (wood + roots and trees + coarse litter + overhanging vegetation + undercut banks + boulder) (%)	159.26 ± 51.95	249.64 ± 109.92	111.80 ± 42.23	160.89 ± 32.03	98.09 ± 42.47	97.08 ± 28.36
	Proportion of undercut banks (%)	0.23 ± 0.24	0 ± 0	0.7 ± 0.22	0.23 ± 0.19	0.48 ± 0.21	0.32 ± 0.27
	Proportion of large cover (wood + trees and roots + coarse litter + overhanging vegetation + undercut banks + boulder) (%)	0.85 ± 0.20	0.94 ± 0.12	0.93 ± 0.07	0.52 ± 0.22	0.67 ± 0.22	0.49 ± 0.23
Catchment variables	Altitude (m)	39.5 ± 9.86	25.1 ± 5.55	119.6 ± 13.47	72 ± 12.81	265.5 ± 70.65	58.71 ± 29.94
	Catchment slope (%)	5.55 ± 1.02	6.85 ± 0.59	5.96 ± 1.05	11.1 ± 1.1	10.23 ± 2.12	10.68 ± 3.16
	Drainage area (km²)	2.19 ± 2.38	9.62 ± 10.64	1.57 ± 2.76	1.13 ± 1.51	11.13 ± 18.24	13.02 ± 17.75
	Proportion of coarse fragments in soil (> 2 mm, %)	0.17 ± 0.42	0.9 ± 0.34	0.1 ± 0.19	0.02 ± 0.04	0.18 ± 0.22	0.56 ± 0.24
	Proportion of silt in soil (%)	1307.88 ± 43.98	1313.9 ± 18.71	1268.6 ± 18.19	1288.7 ± 11.61	1286.4 ± 12.05	1316.29 ± 17.93

The final CAP with local physical habitat variables ($\delta^2 = 0.879$; $p < 0.001$) (Figure 2) selected four axes (Table 2). Streams from different basins had very different physical structures (Pseudo-F = 7.955; $p < 0.001$, see Table S3 for pairwise results). For example, the first CAP axis for Anapu streams showed strong positive correlations with proportion of wood and mean natural cover, and negative correlations with fast channel habitats, undercut banks, and fine substrates (< 16 mm); the opposite pattern occurred in streams of other basins, especially in Juruena, Negro, and Tapajós (Figure 2 a-c). On the second CAP axis, Tapajós and Negro showed strong positive associations with roots, and Capim and Acará were strongly associated with proportion of large cover (Figure 2 a, d, e). Tapajós showed the weakest association with SD thalweg depth on the fourth CAP axis (Figure 2 c, e, f). Generally, streams showed marked differences in environmental heterogeneity levels for physical habitat variables within different basins (F = 5.016; $p = 0.004$; see Table S4 for pairwise results), with higher variability in Anapu (Figure 3).

Table 2. Loadings of the four selected axes of the Canonical Analysis of Principal Coordinates (CAP) with local physical habitat variables of streams. Bold values highlight strong loadings (≥ 0.6).

	CAP1 $\delta = 0.938$	**CAP2** $\delta = 0.880$	**CAP3** $\delta = 0.859$	**CAP4** $\delta = 0.770$
SD thalweg depth	0.250	-0.217	-0.068	**-0.779**
Proportion of silt/muck/clay	-0.039	-0.403	0.489	0.248
Fine substrates	**-0.611**	-0.050	-0.122	-0.112
Proportion of wood	**0.662**	0.231	0.262	0.180
Proportion of roots and trees	-0.199	**0.616**	-0.584	-0.063
Proportion of rapids	-0.519	0.264	0.227	-0.122
Fast channel habitats	**-0.722**	0.074	-0.160	-0.355
SD canopy at banks	-0.415	-0.132	0.276	-0.276
SD barren ground	-0.429	-0.046	0.002	-0.050
Total riparian cover	-0.003	0.549	0.301	-0.471
Mean natural cover	**0.687**	0.203	-0.124	-0.146
Proportion of undercut banks	**-0.600**	-0.526	-0.102	0.077
Proportion of large cover	0.392	**-0.621**	-0.073	0.188
Number of large woody pieces inside + above channel / m^2 - size class 1	0.208	0.010	-0.438	-0.009
Volume of large woody pieces inside + above channel / m^2 - size class 4	0.174	-0.087	0.185	-0.070

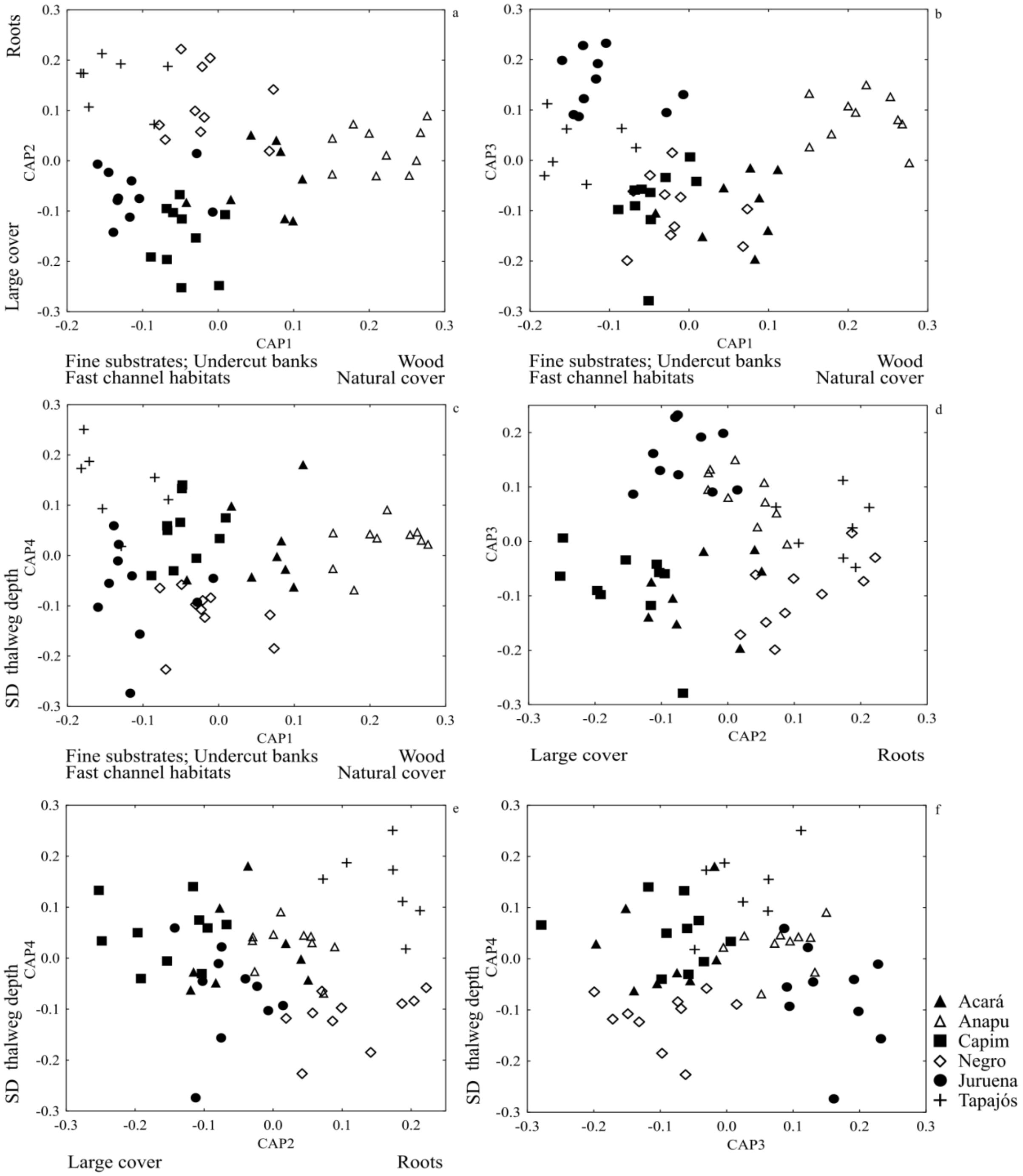

Figure 2. Resulting ordination of Canonical Analysis of Principal Coordinates (CAP) with local physical habitat variables of 55 streams distributed in six river basins of the Amazon.

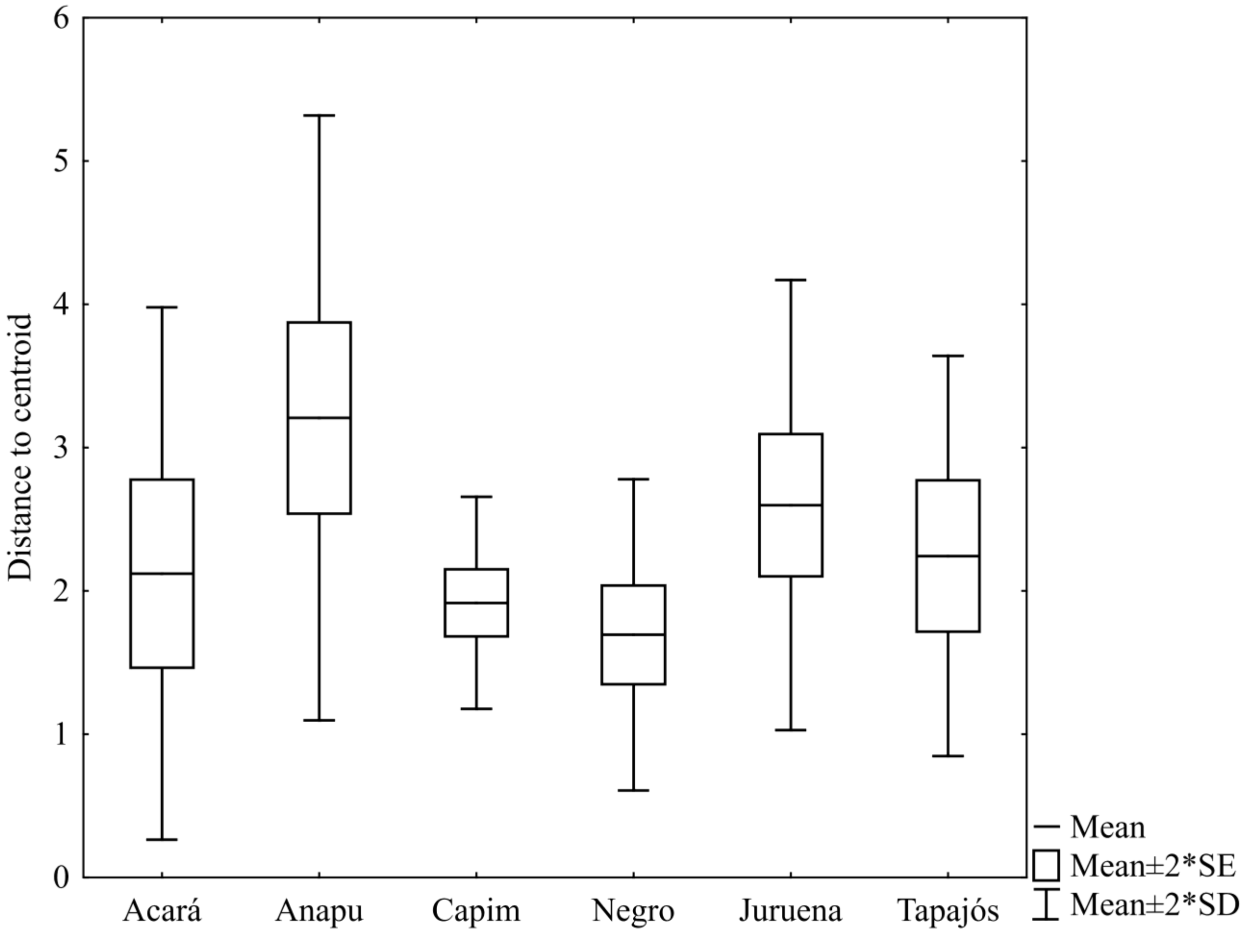

Figure 3. Result of Permutational Analysis of Multivariate Dispersions (PERMDISP) with local physical habitat variables of 55 streams distributed in six river basins of the Amazon.

Three axes with catchment metrics ($\delta^2 = 0.928$; $p < 0.001$) were selected by CAP, all with correlated variables (Table 3). River basins showed different patterns of environmental structure at the catchment scale (Pseudo-F = 10.649; $p < 0.001$, see Table S3 for pairwise results) (Figure 4). For example, streams close to Amazon lowlands, such as Acará and Anapu, had lower altitudes and slope, and these variables increase towards the Brazilian and Guiana Shields, as observed in Juruena, Tapajós, and Negro streams (Figure 4 a-b). Anapu and Tapajós showed positive association with proportion of coarse fragments (Figure 4 c). Environmental heterogeneity showed different levels for catchment variables in streams of different basins (F = 3.464; $p = 0.024$, see Table S4 for pairwise results). The Juruena and Tapajós basins showed the greatest heterogeneity in catchment characteristics among small streams (Figure 5).

Table 3. Loadings of the two first axes of Canonical Analysis of Principal Coordinates (CAP) with catchment variables of 55 streams distributed in six river basins of the Amazon. Bold values highlight strong loadings (≥ 0.6).

	CAP1	**CAP2**	**CAP3**
	δ = 0.963	δ = 0.834	δ = 0.754
Altitude	**0.966**	0.246	0.052
Slope	0.487	**-0.785**	-0.338
Drainage area	-0.057	-0.382	0.503
Coarse fragments	-0.374	-0.503	**0.753**
Silt	0.219	0.285	0.235

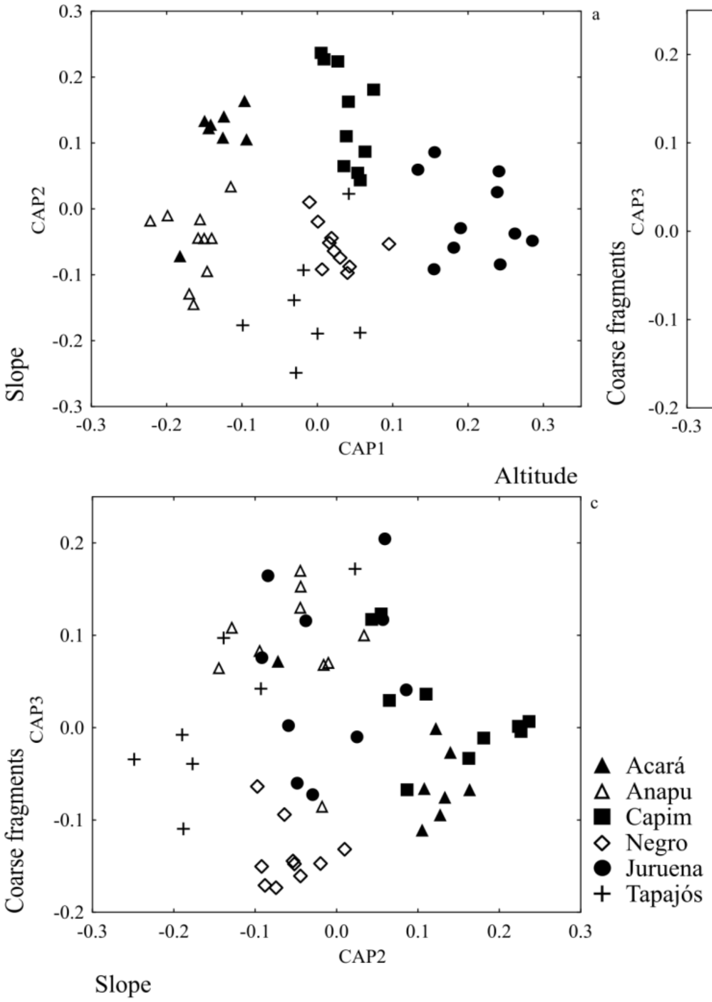

Figure 4. Resulting ordination of Canonical Analysis of Principal Coordinates (CAP) with catchment variables of 55 streams distributed in six river basins of the Amazon.

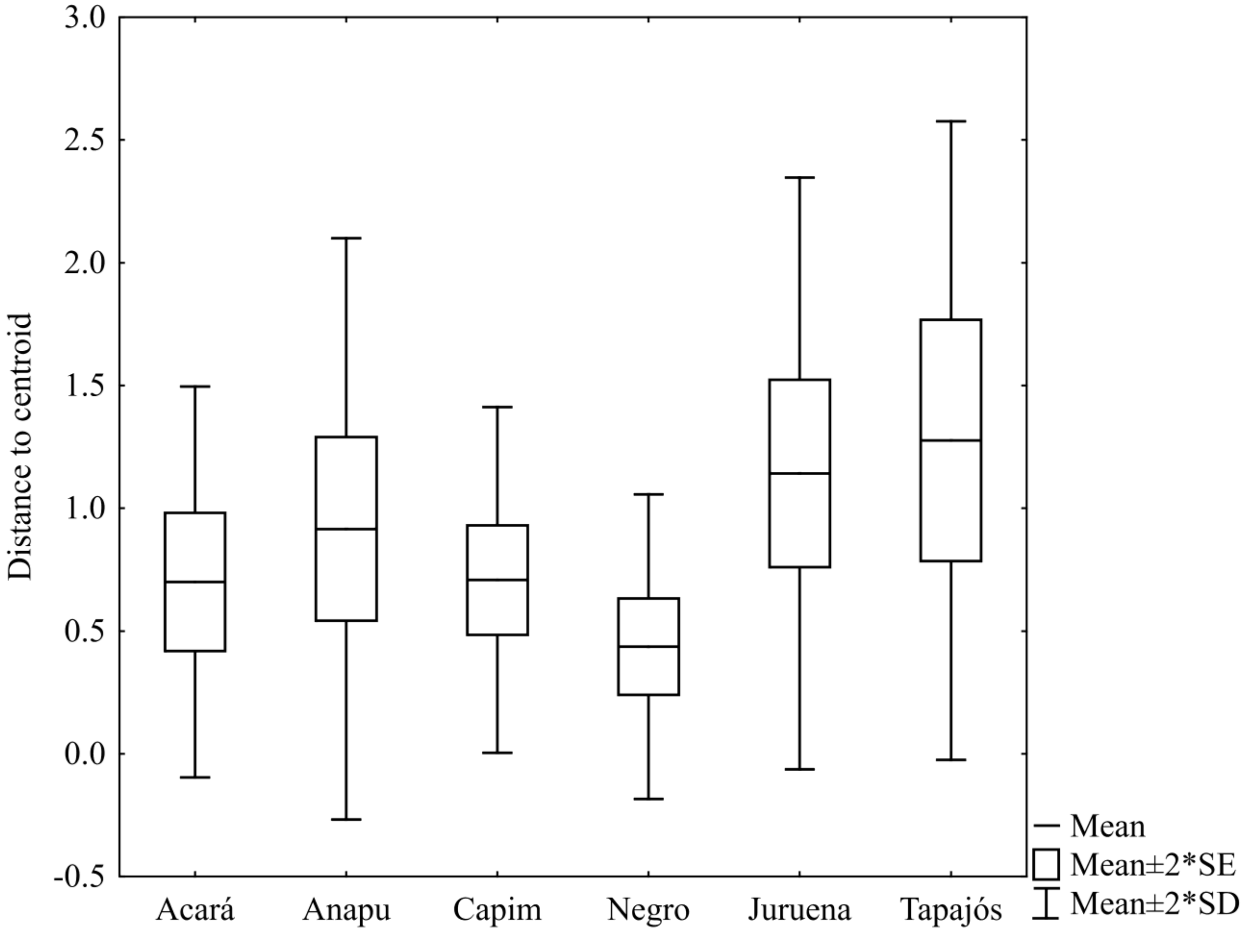

Figure 5. Result of Permutational Analysis of Multivariate Dispersions (PERMDISP) with catchment variables of 55 streams distributed in six river basins of the Amazon.

After the two CAPs, eight local physical habitat variables and three catchment variables remained. Multiple regressions showed that these three remaining catchment metrics – altitude, catchment slope, and coarse fragments in basin soils – were important drivers of local physical structure of streams, and altitude played a central role in nearly all cases (Table 4). These variables influence current velocity, substrate, and instream cover.

Table 4. Results of multiple regressions between local and catchment variables of 55 streams distributed in six river basins of the Amazon. Bold values indicate significant values at α ≤ 0.05. SE = standard error.

Local variable	Multiple regression	Catchment variables	β	SE of β	t	p
SD thalweg depth	$R^2= 0.059$; $F_{(1,53)} = 3.345$, $p = 0.073$	Coarse fragments	-0.244	0.133	-1.829	0.073
Fine substrates	$R^2 = 0.227$; $F_{(3,51)} = 4.994$, $p = 0.004$	Altitude	0.337	0.144	2.345	**0.023**
		Coarse fragments	-0.159	0.139	-1.144	0.258
		Slope	0.129	0.128	1.008	0.318
Proportion of wood	$R^2 = 0.445$; $F_{(3,51)} = 13.658$, $p < 0.001$	Altitude	**-0.441**	**0.122**	**-3.615**	**<0.001**
		Coarse fragments	**0.349**	**0.118**	**2.958**	**0.005**
		Slope	0.157	0.108	1.452	0.153
Proportion of roots and trees	$R^2 = 0.295$; $F_{(3,51)} = 7.139$, $p < 0.001$	Slope	**0.371**	**0.122**	**3.035**	**0.004**
		Altitude	**-0.506**	**0.137**	**-3.684**	**<0.001**
		Coarse fragments	**-0.444**	**0.133**	**-3.340**	**0.002**
Fast channel habitats	$R^2 = 0.39$; $F_{(3,51)} = 10.887$, $p < 0.001$	Altitude	**0.306**	**0.128**	**2.397**	**0.020**
		Slope	**0.386**	**0.114**	**3.399**	**0.001**
		Coarse fragments	-0.186	0.124	-1.504	0.139
Mean natural cover	$R^2 = 0.323$; $F_{(1,53)} = 25.276$, $p < 0.001$	Altitude	**-0.568**	**0.113**	**-5.028**	**<0.001**
Undercut banks	$R^2 = 0.394$; $F_{(1,53)} = 34.555$, $p < 0.001$	Altitude	**0.628**	**0.107**	**5.878**	**<0.001**
Large cover	$R^2 = 0.205$; $F_{(2,52)} = 6.708$, $p = 0.002$	Slope	**-0.433**	**0.124**	**-3.502**	**<0.001**
		Coarse fragments	0.128	0.124	1.036	0.305

DISCUSSION

Our results showed high heterogeneity among streams in both their local physical habitat structure as well as their catchment characteristics, and their strong associations confirmed the importance of regional metrics at catchment scale as predictors of local variables. According to our results, altitude is the main driver of variation in local physical habitats, and is closely related to flow. The interaction of altitude and slope with substrate and flow velocity explained most of the environmental structures of streams, separating flat, low altitudinal river basins with slow flowing waterbodies, e.g. Anapu and Acará streams, from fast flowing sites with steeper slopes and higher altitude basins, such as Juruena and Negro streams.

Variations in altitude and slope can cause several changes across the longitudinal gradient due to their influence in flow velocity, one of the most important local structural stream variables, leading to several changes across the longitudinal gradient (Vannote *et al.*, 1980; Snelder and Biggs, 2002; Grabowski *et al.*, 2014), altering channel morphology, bank erosion and mobilization, transportation and deposition of sediments and substrates (Florsheim *et al.*, 2008; Grabowski *et al.*, 2014; Schneider *et al.*, 2015). Our results showed that sites with high altitude and steeper slopes had lower proportion of wood and large cover, which can be linked to higher rates of sediment transport because of higher flows and shear stress (Grabowski *et al.*, 2014). The positive association between altitude and velocity also affects channel morphology (Schneider *et al.*, 2015), because enhanced shear stress, especially during floods, increases bank erosion and creates undercut banks (Florsheim *et al.*, 2008), which were also correlated with altitude. Other studies showed similar results (Richards *et al.*, 1996; Mugodo *et al.*, 2006), highlighting the importance of altitude and slope as drivers of physical habitat variation in small streams.

Due to the natural impoundment in Anapu basin, its waterbodies have lacustrine characteristics typical of ria lakes, which are sections of drowned valleys in Amazonian affluents formed after sea level changes during Holocene (Sioli, 1967; Behling and Costa, 2000). Under this condition, low current velocity leads to low shear stress values, preventing transport of bed substrates downstream and allowing accumulation of organic matter throughout the longitudinal gradient (Hoover *et al.*, 2006). Other river basins showed higher flow heterogeneity, with higher rates of substrate transportation and higher exposure of sand-covered streambeds. Since this more intense, heterogeneous flow is also responsible for excavating undercut banks, this explains why these banks are absent in the streams of Anapu Basin. This microhabitat results from erosive processes, and is involved with stream channel morphology; it can intensify meander formation, and is used as cover for aquatic organisms (Florsheim *et al.*, 2008).

Increased proportion of coarse fragments in basin soils also affects flow velocity, because it enhances stream bed roughness and water percolation, increasing flow resistance and reducing runoff and flow velocity (Beibei *et al.*, 2009; Schneider *et al.*, 2015). Slow flowing streams with great accumulation of wood showed negative association with coarse fragments in soil, possibly due to reduced velocity. Another outcome is the lower proportion of roots in soils rich in coarse fragments, which are harder to penetrate by plant roots. Initial roots must first mechanically break rocks to provide easier access to new plant roots (Pawlik *et al.*, 2016).

Environmental heterogeneity patterns within basins were not the same at different scales, indicating that different processes act on each scale, which reflects the complex nature of drainage systems. At a large scale, basins with high heterogeneity in catchment-scale variables were closer to Brazilian and Guiana Shields, with higher altitudes and steeper slopes. As explained before, these features are responsible for several characteristics of channel gradients (Grabowski *et al.*, 2014; Schneider *et al.*, 2015). Locally, high heterogeneity in physical habitat variables is highest in streams that are in river basins with low altitude and low slope; this instream heterogeneity is due to variations in substrates, reflecting variations in riparian cover, stream size, incision and lateral erosion, and stream power (Rigon *et al.*, 2012). These spatial differences in heterogeneity emphasize how difficult it is to choose the most relevant spatial scale in ecological studies. Leal *et al.* (2016) pointed out the different responses of instream habitat variables to land use changes and large-scale variables in the Amazon Basin, while Fernandes *et al.* (2013) showed that local and regional variables play different roles on fish assemblage attributes.

Conclusions

Considering that human impacts are increasing at high rates in the Amazon and that small streams are the most affected watercourses (Thieme *et al.*, 2007; Davidson *et al.*, 2012; Leal *et al.*, 2016), it is important to characterize the natural conditions of streams. Our results highlighted the high environmental heterogeneity both in physical habitat and catchment variables of such waterbodies in the Amazon Basin and pointed out some links between local and regional scales; moreover, our results provide parameters for the reference conditions of small streams.

Impact mitigation techniques and the creation of protected areas aiming at lotic systems, a practice still unusual in the Amazon (Castello *et al.*, 2013), must consider both local and regional settings for better strategic planning. To protect biodiversity, for example, the fact that aquatic fauna is extremely dependent on the environmental structure of waterbodies must be considered (Vannote *et al.*, 1980; Wang *et al.*, 2003; Kemenes *et al.*, 2010; Frederico *et al.*, 2014; Kemenes and Forsberg, 2014; Portocarrero-Aya and Cowx, 2016), as well as the fact that natural variations across the Amazon Basin are one of the reasons behind its high diversity (Junk *et al.*, 2007; Castello *et al.*, 2013). Therefore, the creation of protected areas surrounding river basins should involve the highest possible variability of environmental conditions to capture high variations in species composition. We hope these results serve as a basis to support more efficient monitoring projects and restoration practices, establishing better scenarios for the future of the Amazon.

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SUPPLEMENTARY MATERIAL

Table S1. Local and catchment variables used to characterize 55 streams in six river basins in Amazon. The method of exclusion applied to each variable is supplied. CV = coefficient of variation; CAP = Canonical Analysis of Principal Coordinates.

Block of variables	Variable name	Code	Acará	Anapu	Capim	Negro	Juruena	Tapajós	Exclusion
Channel morphology	Mean depth of transection (cm)	XDEPTH_TR	17.13 ± 8.36	39.07 ± 12.12	15.02 ± 7.01	20.56 ± 8.34	26.26 ± 18.02	21.01 ± 6.86	Correlation
	SD depth of transection (cm)	SDDEPTH_TR	11.44 ± 4.79	15.61 ± 3.16	10.12 ± 4.11	13.44 ± 5.21	14.33 ± 9.12	12.32 ± 4.91	Correlation
	Mean depth of thalweg (cm)	XDEPTH_TH	30.17 ± 14.29	54.36 ± 15.96	25.58 ± 11.09	31.41 ± 13.63	38.99 ± 29.87	10.71 ± 2.94	Correlation
	SD depth of thalweg (cm)	SDDEPTH_TH	9.16 ± 3.83	11.35 ± 2.06	10.58 ± 2.72	13.92 ± 3.29	11.52 ± 5.88	2.59 ± 0.58	Retained
	Mean wetted width (m)	XWIDTH	3.45 ± 1.2	4.52 ± 2.06	2.25 ± 0.54	2.01 ± 0.59	4.07 ± 3.14	0.96 ± 0.51	Correlation
	SD wetted width (m)	SDWIDTH	0.76 ± 0.41	1.33 ± 1	0.67 ± 0.25	0.58 ± 0.19	0.96 ± 0.64	1.11 ± 0.98	CAP per block
	Mean wetted area of transection (width x depth) (m^2)	XWXD_P	0.63 ± 0.47	1.73 ± 0.74	0.37 ± 0.24	0.43 ± 0.29	1.55 ± 1.95	0.59 ± 0.25	Correlation
	SD wetted area of transection (width x depth) (m^2)	SDWXD_P	0.22 ± 0.13	0.66 ± 0.45	0.18 ± 0.1	0.23 ± 0.11	0.45 ± 0.52	0.3 ± 0.14	Correlation
	Mean transection width x depth ratio (m/m)	XWD_RAT_P	26.19 ± 14.72	13.7 ± 8.12	19.19 ± 5.27	14.06 ± 4.06	17.86 ± 4.82	15.39 ± 7.52	Correlation
	SD transection width x depth ratio (m/m)	SDWD_RAT_P	10.3 ± 8.65	5.59 ± 5.76	7.33 ± 2.72	7.92 ± 3.45	8.45 ± 4.81	7.88 ± 6.01	Correlation

	Mean wetted area of longitudinal section (m^2)	XWXD	1.14 ± 0.89	2.46 ± 1.16	0.64 ± 0.43	0.71 ± 0.5	2.39 ± 3.28	0.96 ± 0.51	CAP per block
	Mean longitudinal section width x depth ratio (m/m)	XWD_RAT	13.09 ± 6.59	8.96 ± 4.66	9.49 ± 1.89	7.15 ± 1.45	10.56 ± 2.47	7.65 ± 2.24	CAP per block
Substrate	Mean embeddedness (channel + banks) (%)	XEMBED	44.68 ± 24.65	62.25 ± 21.86	53.3 ± 14.63	61.07 ± 11.76	69.93 ± 14.87	66.13 ± 10.89	Correlation
	SD embeddedness (channel + banks) (%)	VEMBED	35.3 ± 9.86	30.79 ± 6.74	39.14 ± 2.5	39.61 ± 4.03	32.93 ± 7.56	41.35 ± 5.5	Correlation
	Mean embeddedness (channel) (%)	XCEMBED	48.01 ± 27.27	66.64 ± 21.46	53.32 ± 17.54	67.15 ± 13.09	64.44 ± 19.15	70.65 ± 10.34	CAP per block
	SD embeddedness (channel) (%)	VCEMBED	35.14 ± 9.66	30.12 ± 6.48	37.4 ± 3.49	38.6 ± 5.16	32.27 ± 7.93	41.39 ± 5.84	CAP per block
	Smooth bedrock (%)	PCT_SR	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	0 > 80 %
	Rough bedrock (%)	PCT_RR	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	0.29 ± 0.64	0 ± 0	0 > 80 %
	Bedrock (smooth + rough) (%)	PCT_BDRK	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	0.38 ± 0.8	0 ± 0	0 > 80 %
	Large boulder (%)	PCT_LB	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.48 ± 1.51	0 ± 0	0 > 80 %
	Small boulder (%)	PCT_SB	0.5 ± 1.41	0 ± 0	0.95 ± 1.9	0 ± 0	2.57 ± 4.45	0 ± 0	0 > 80 %
	Boulder (large + small) (%)	PCT_BL	0.5 ± 1.41	0 ± 0	0.95 ± 1.9	0 ± 0	3.05 ± 5.04	0 ± 0	0 > 80 %
	Cobble (%)	PCT_CB	0.17 ± 0.47	0 ± 0	2.38 ± 5.14	0 ± 0	2.48 ± 4.24	0.41 ± 0.75	0 > 80 %
	Coarse gravel (%)	PCT_CG	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	2.57 ± 5.66	2.48 ± 2.72	0 > 80 %

Substrate > 16mm diameter (bedrock, boulder, cobble and coarse gravel) (%)	PCT_BIGR	0.67 ± 1.43	0 ± 0	3.52 ± 5.7	0 ± 0	8.48 ± 10.4	2.89 ± 2.78	Correlation
Fine gravel (%)	PCT_FG	0.17 ± 0.47	0 ± 0	6.01 ± 8.61	0 ± 0	3.45 ± 3.99	1.52 ± 1.46	CAP per block
Sand (%)	PCT_SA	30.5 ± 14.51	0 ± 0	22.16 ± 19.2	38.09 ± 11.69	31.44 ± 19.11	36.99 ± 19.09	Retained
Silt/muck/clay (%)	PCT_ST	6.5 ± 3.73	26.1 ± 31.18	9.59 ± 6.97	0.67 ± 1.01	20.09 ± 9.44	10.8 ± 17	Retained
Substrate < 16 mm diameter (fine gravel, sand and silt/muck/clay) (%)	PCT_SFGF	37.17 ± 13.55	26.1 ± 31.18	37.76 ± 12.06	38.75 ± 11.62	54.98 ± 15.34	49.3 ± 11.37	CAP per block
Total organic matter (litter, wood, roots and algae) (%)	PCT_ORG	60.83 ± 14.36	72.95 ± 30.51	51.34 ± 10.16	61.06 ± 11.59	34.83 ± 21.48	47.81 ± 12.71	CAP per block
Wood (%)	PCT_WD	6.5 ± 4.3	21.14 ± 8.18	5.1 ± 4.29	5.27 ± 2.17	4.7 ± 3.75	5.88 ± 2.52	Retained
Hardpan (%)	PCT_HP	1 ± 1.55	0 ± 0	7.37 ± 7.82	0 ± 0	0.95 ± 2.42	0 ± 0	CAP per block
Roots (%)	PCT_RO	7.67 ± 4.98	6.86 ± 9.64	6.48 ± 4.7	36.57 ± 9.76	3.05 ± 4.51	22.36 ± 7.59	Retained
Fine litter (%)	PCT_FL	30 ± 16.9	17.05 ± 15.83	11.41 ± 11.46	8.42 ± 4.75	6.83 ± 5.93	10.78 ± 8.92	CAP per block
Coarse litter (%)	PCT_CL	16.67 ± 6.09	27.9 ± 23.33	28.26 ± 10.77	10.8 ± 4.32	20.26 ± 16.76	8.8 ± 6.58	CAP per block
Filamentous algae (%)	PCT_FA	0 ± 0	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	0 > 80 %

	Macrophytes (%)	PCT_MA	0.17 ± 0.47	0.95 ± 2.2	0 ± 0	0.1 ± 0.3	0.76 ± 2.41	0 ± 0	0 > 80 %
Channel habitats units	Falls (%)	PCT_FA	0 ± 0	0 ± 0	0.07 ± 0.21	0 ± 0	0.07 ± 0.21	0 ± 0	0 > 80 %
	Cascades (%)	PCT_CA	0 ± 0	0 ± 0	0 ± 0	0.13 ± 0.28	0.07 ± 0.21	0.1 ± 0.25	0 > 80 %
	Rapids (%)	PCT_RA	0.08 ± 0.24	0 ± 0	0.6 ± 0.58	3.67 ± 4.8	13.67 ± 20.97	10.98 ± 15.19	Retained
	Riffles (%)	PCT_RI	34.53 ± 30.52	7.53 ± 22.45	23.13 ± 17.57	50.87 ± 17.16	50.4 ± 23.04	35.88 ± 29.05	Correlation
	Glides (%)	PCT_GL	58.97 ± 25.81	92 ± 22.76	69.4 ± 14.9	45 ± 18.08	33.93 ± 30.14	41.71 ± 26.17	Correlation
	Impoundment pool (%)	PCT_IP	1.92 ± 3.89	0.13 ± 0.42	1.2 ± 3.57	0 ± 0	0 ± 0	8.1 ± 6.22	0 > 80 %
	Plunge pool (%)	PCT_PP	0 ± 0	0 ± 0	0.4 ± 1.26	0 ± 0	0 ± 0	0 ± 0	0 > 80 %
	Lateral scour pool (%)	PCT_LP	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	CV
	Trench pool (%)	PCT_TP	4.5 ± 6.65	0.33 ± 0.57	5.2 ± 5.22	0.33 ± 0.57	1.87 ± 2.49	3.24 ± 6.6	Correlation
	Backwater pool (%)	PCT_BP	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	CV
	Fast channel habitats (FA+CA+RA+RI) (%)	PCT_FAST	34.61 ± 30.55	7.53 ± 22.45	23.8 ± 17.62	54.67 ± 18.1	64.2 ± 31.03	46.95 ± 29.44	Retained
	Slow channel habitats (GL+ All pool types) (%)	PCT_SLOW	65.39 ± 30.55	92.47 ± 22.45	76.2 ± 17.62	45.33 ± 18.1	35.8 ± 31.03	53.05 ± 29.44	CAP per block
	All pool types (%)	PCT_POOL	6.42 ± 9.69	0.47 ± 0.63	6.8 ± 5.8	0.33 ± 0.57	1.87 ± 2.49	11.33 ± 7.24	CAP per block

	Sequence fast flow, slow flow, and pools (1= maximum heterogeneity, 0= maximum homogeneity)	SEQ_FLO_1	0.13 ± 0.08	0.02 ± 0.04	0.16 ± 0.06	0.16 ± 0.08	0.12 ± 0.1	0.08 ± 0.05	Correlation
	Sequence fast and slow flow	SEQ_FLO_2	0.1 ± 0.09	0.02 ± 0.04	0.13 ± 0.06	0.16 ± 0.08	0.11 ± 0.09	0.06 ± 0.04	CAP per block
Riparian vegetation cover	Mean canopy density channel (%)	XCDENMID	97.28 ± 1.34	93.9 ± 3.2	89.76 ± 4.38	93.7 ± 2.03	83.52 ± 10.36	96.35 ± 1.81	CV
	SD canopy density channel (%)	SDCDENMID	2.38 ± 0.6	4.5 ± 2.73	5.87 ± 4.2	4.42 ± 1.51	9.45 ± 6.15	3.77 ± 2.25	Correlation
	Mean canopy density banks (%)	XCDENBANK	98.43 ± 0.96	96.79 ± 2.53	94.41 ± 4.03	95.7 ± 1.54	89.63 ± 3.41	96.87 ± 0.97	CV
	SD canopy density banks (%)	SDCDENBANK	2.69 ± 1.35	3.62 ± 2.59	5.98 ± 4.62	4.87 ± 1.81	9.19 ± 6.03	4.39 ± 1.57	Retained
	Mean canopy cover	XC	1.08 ± 2.04	0.59 ± 1.79	2.01 ± 2.57	5.07 ± 6.38	4.34 ± 2.19	1.22 ± 1.44	Correlation
	SD canopy cover	SDC	1.22 ± 2.06	0.5 ± 1.32	2.21 ± 2.54	3.06 ± 4.88	2.41 ± 1.72	3.3 ± 4.64	CAP per block
	Mean understory cover	XM	82.13 ± 28.64	73.76 ± 11.55	67.77 ± 13.59	82.99 ± 12.33	87.75 ± 15.11	94.59 ± 17.72	Correlation
	SD understory cover	SDM	26.38 ± 6.25	18.21 ± 4.93	23 ± 4.26	22.46 ± 6.51	25.4 ± 9.2	23.15 ± 6.19	CAP per block
	Mean ground cover	XG	67.54 ± 22.76	93.05 ± 18.66	71.99 ± 14.39	96.31 ± 16.29	90.05 ± 16.89	83.08 ± 12.21	Correlation
	SD ground cover	SDG	20.88 ± 7.31	25.01 ± 11.79	21.64 ± 8.21	16.47 ± 5.37	22.32 ± 8.39	14.55 ± 2.72	CAP per block
	Mean barren ground	XGB	50.82 ± 25.17	70.78 ± 24.9	40.59 ± 6.33	85.86 ± 21.18	64.73 ± 11.96	53.17 ± 7.53	Correlation

	SD barren ground	SDGB	15.96 ± 4.72	19.82 ± 6.33	17.24 ± 3.53	17.44 ± 5.77	22.18 ± 6.68	23.65 ± 6.82	Retained
	Mean canopy + understory	XCM	149.67 ± 44.63	166.81 ± 21.7	139.76 ± 18.81	179.3 ± 25.14	177.8 ± 24.03	177.68 ± 21.2	Correlation
	SD canopy + understory	SDCM	30.11 ± 10.88	32.85 ± 13.96	28.4 ± 5.48	27.49 ± 9.59	36.92 ± 15.37	27.17 ± 6.97	Correlation
	Mean total riparian cover	XCMG	200.5 ± 56.2	237.59 ± 34.21	180.35 ± 23.07	265.16 ± 41.55	242.52 ± 31.14	230.84 ± 24.86	Retained
	SD total riparian cover	SDCMG	32.16 ± 6.62	39.36 ± 17.06	34.53 ± 5.87	37.52 ± 13.87	43.45 ± 21.12	37.44 ± 8	CAP per block
Large woody pieces	Number LWP inside bankfull channel / 100m - size class 1	C1W_100	50.58 ± 30.84	33.47 ± 21.11	20.73 ± 13.25	21.07 ± 9	20 ± 13.36	10.86 ± 3.52	Correlation
	Number LWP inside bankfull channel / 100m - size class 2	C2W_100	7.92 ± 3.81	15.2 ± 8.35	3.6 ± 3.61	2.93 ± 0.9	7.47 ± 6.33	2.38 ± 2.21	Correlation
	Number LWP inside bankfull channel / 100m - size class 3	C3W_100	3.58 ± 2.96	4.87 ± 3.61	0.87 ± 1.18	0.6 ± 0.58	2.13 ± 2.01	0.38 ± 0.52	Correlation
	Number LWP inside bankfull channel / 100m - size class 4	C4W_100	1.25 ± 1.15	1.6 ± 1.48	0.13 ± 0.42	0.13 ± 0.28	0.67 ± 0.77	0 ± 0	Correlation
	Number LWP inside bankfull channel / 100m - size class 5	C5W_100	0.08 ± 0.24	0.47 ± 0.83	0 ± 0	0 ± 0	0.07 ± 0.21	0 ± 0	0 > 80 %
	Volume LWP inside bankfull channel / 100m - size class 1	V1W_100	12.93 ± 10.16	22.3 ± 22.74	2.81 ± 2.28	2.78 ± 1.53	9.28 ± 8.66	1.32 ± 0.67	Correlation

Volume LWP inside bankfull channel / 100m - size class 2	V2W_100	9.21 ± 11.2	21.24 ± 22.93	1.02 ± 1.72	1.72 ± 1.52	7.05 ± 7.43	0.34 ± 0.43	Correlation
Volume LWP inside bankfull channel / 100m - size class 3	V3W_100	10.45 ± 11.27	17.89 ± 22.34	1.82 ± 2.04	1.08 ± 1.51	8.56 ± 8.51	0.83 ± 0.65	Correlation
Volume LWP inside bankfull channel / 100m - size class 4	V4W_100	7.08 ± 10.09	13.94 ± 19.83	0.33 ± 1.05	0.63 ± 1.51	4.91 ± 6.14	0 ± 0	Correlation
Volume LWP inside bankfull channel / 100m - size class 5	V5W_100	1.89 ± 5.33	10.56 ± 18.88	0 ± 0	0 ± 0	1.51 ± 4.77	0 ± 0	0 > 80 %
Number LWP above bankfull channel / 100m - size class 1	C1D_100	13.67 ± 10.13	7.27 ± 4.42	6.47 ± 2.25	7.53 ± 3.22	5.93 ± 3.35	5.33 ± 1.85	Correlation
Number LWP above bankfull channel / 100m - size class 2	C2D_100	4.25 ± 1.78	5.27 ± 4.2	2.33 ± 2.09	4.07 ± 2.94	4 ± 2.06	2 ± 1.49	Correlation
Number LWP above bankfull channel / 100m - size class 3	C3D_100	2.17 ± 0.99	2.8 ± 2.66	1.8 ± 1.99	1.73 ± 1.55	2.33 ± 2.09	0.86 ± 0.74	Correlation
Number LWP above bankfull channel / 100m - size class 4	C4D_100	1.17 ± 1.11	1.4 ± 1.92	0.47 ± 0.71	0.6 ± 0.86	0.93 ± 0.84	0.19 ± 0.33	Correlation
Number LWP above bankfull channel / 100m - size class 5	C5D_100	0.33 ± 0.5	0.33 ± 0.85	0 ± 0	0.2 ± 0.63	0.27 ± 0.47	0 ± 0	0 > 80 %
Volume LWP above bankfull channel / 100m - size class 1	V1W_100	11.84 ± 10.26	16.4 ± 26.58	3.14 ± 3.29	7.44 ± 13.81	11.57 ± 10.1	1.99 ± 1.75	Correlation

Volume LWP above bankfull channel / 100m - size class 2	V2W_100	11.29 ± 10.21	16.28 ± 26.6	2.9 ± 3.32	7.24 ± 13.76	11.46 ± 10.07	1.79 ± 1.86	Correlation
Volume LWP above bankfull channel / 100m - size class 3	V3W_100	10.82 ± 10.15	15.09 ± 26.11	2.77 ± 3.32	6.8 ± 13.88	11.06 ± 10.02	1.48 ± 1.85	Correlation
Volume LWP above bankfull channel / 100m - size class 4	V4W_100	10.03 ± 10.65	13.03 ± 26.32	1.49 ± 2.11	5.93 ± 14.04	9.6 ± 9.87	0.9 ± 1.77	Correlation
Volume LWP above bankfull channel / 100m - size class 5	V5W_100	7.54 ± 11.4	7.54 ± 19.14	0 ± 0	4.52 ± 14.31	6.03 ± 10.54	0 ± 0	0 > 80 %
Number LWP inside + above / 100m - size class 1	C1T_100	64.25 ± 39.65	40.73 ± 22.27	27.2 ± 14.03	28.6 ± 10.14	25.93 ± 13.38	16.19 ± 4.89	Correlation
Number LWP inside + above / 100m - size class 2	C2T_100	12.17 ± 3.66	20.47 ± 10.72	5.93 ± 4.35	7 ± 3.3	11.47 ± 7.07	4.38 ± 2.95	Correlation
Number LWP inside + above / 100m - size class 3	C3T_100	5.75 ± 3.34	7.67 ± 5.92	2.67 ± 2.55	2.33 ± 1.76	4.47 ± 3.17	1.24 ± 1.05	Correlation
Number LWP inside + above / 100m - size class 4	C4T_100	2.42 ± 1.92	3 ± 3.08	0.6 ± 0.86	0.73 ± 0.86	1.6 ± 1	0.19 ± 0.33	Correlation
Number LWP inside + above / 100m - size class 5	C5T_100	0.42 ± 0.5	0.8 ± 1.53	0 ± 0	0.2 ± 0.63	0.33 ± 0.57	0 ± 0	0 > 80 %
Volume LWP inside + above / 100m - size class 1	V1T_100	24.76 ± 11.75	38.7 ± 45.26	5.95 ± 4.57	10.21 ± 13.71	20.86 ± 13.45	3.31 ± 2.01	Correlation

Volume LWP inside + above / 100m - size class 2	V2T_100	21.74 ± 13.05	37.52 ± 45.57	4.72 ± 4.68	8.96 ± 13.46	20.02 ± 13.64	2.62 ± 2.13	Correlation
Volume LWP inside + above / 100m - size class 3	V3T_100	20.03 ± 13.15	32.98 ± 45.08	3.79 ± 4.56	7.88 ± 13.62	18.11 ± 12.86	1.82 ± 2.08	Correlation
Volume LWP inside + above / 100m - size class 4	V4T_100	17.11 ± 12.94	26.97 ± 42.36	1.83 ± 2.82	6.57 ± 13.85	14.51 ± 11.98	0.9 ± 1.77	Correlation
Volume LWP inside + above / 100m - size class 5	V5T_100	9.43 ± 11.22	18.1 ± 34.68	0 ± 0	4.52 ± 14.31	7.54 ± 12.82	0 ± 0	0 > 80 %
Number LWP inside bankfull channel / m2 - size class 1	C1W_MSQ	0.18 ± 0.13	0.08 ± 0.04	0.09 ± 0.06	0.1 ± 0.04	0.05 ± 0.02	0.04 ± 0.02	Correlation
Number LWP inside bankfull channel / m2 - size class 2	C2W_MSQ	0.02 ± 0.01	0.04 ± 0.02	0.01 ± 0.01	0.01 ± 0	0.02 ± 0.02	0.01 ± 0.01	Correlation
Number LWP inside bankfull channel / m2 - size class 3	C3W_MSQ	0.01 ± 0.01	0.01 ± 0.01	0 ± 0	0 ± 0	0.01 ± 0.01	0 ± 0	Correlation
Number LWP inside bankfull channel / m2 - size class 4	C4W_MSQ	0 ± 0	0 ± 0.01	0 ± 0	0 ± 0	0 ± 0	0 ± 0	Correlation
Number LWP inside bankfull channel / m2 - size class 5	C5W_MSQ	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 > 80 %
Volume LWP inside bankfull channel / m2 - size class 1	V1W_MSQ	0.04 ± 0.03	0.07 ± 0.07	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.03	0.01 ± 0	Correlation

Volume LWP inside bankfull channel / m2 - size class 2	V2W_MSQ	0.03 ± 0.03	0.06 ± 0.07	0 ± 0.01	0.01 ± 0.01	0.02 ± 0.03	0 ± 0	Correlation
Volume LWP inside bankfull channel / m2 - size class 3	V3W_MSQ	0.03 ± 0.03	0.06 ± 0.07	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.03	0 ± 0	Correlation
Volume LWP inside bankfull channel / m2 - size class 4	V4W_MSQ	0.02 ± 0.03	0.05 ± 0.07	0 ± 0	0 ± 0.01	0.02 ± 0.03	0 ± 0	Correlation
Volume LWP inside bankfull channel / m2 - size class 5	V5W_MSQ	0.01 ± 0.02	0.03 ± 0.06	0 ± 0	0 ± 0	0.01 ± 0.03	0 ± 0	0 > 80 %
Number LWP above bankfull channel / m2 - size class 1	C1D_MSQ	0.05 ± 0.04	0.02 ± 0.02	0.03 ± 0.01	0.04 ± 0.02	0.02 ± 0.02	0.02 ± 0.01	Correlation
Number LWP above bankfull channel / m2 - size class 2	C2D_MSQ	0.01 ± 0.01	0.02 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	Correlation
Number LWP above bankfull channel / m2 - size class 3	C3D_MSQ	0.01 ± 0	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0 ± 0	Correlation
Number LWP above bankfull channel / m2 - size class 4	C4D_MSQ	0 ± 0	0.01 ± 0.01	0 ± 0	0 ± 0.01	0 ± 0	0 ± 0	Correlation
Number LWP above bankfull channel / m2 - size class 5	C5D_MSQ	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 > 80 %
Volume LWP above bankfull channel / m2 - size class 1	V1W_MSQ	0.04 ± 0.03	0.06 ± 0.11	0.01 ± 0.01	0.04 ± 0.07	0.05 ± 0.06	0.01 ± 0.01	Correlation

Volume LWP above bankfull channel / m2 - size class 2	V2W_MSQ	0.04 ± 0.03	0.06 ± 0.11	0.01 ± 0.01	0.04 ± 0.07	0.05 ± 0.06	0.01 ± 0.01	Correlation
Volume LWP above bankfull channel / m2 - size class 3	V3W_MSQ	0.03 ± 0.03	0.06 ± 0.11	0.01 ± 0.01	0.04 ± 0.07	0.05 ± 0.06	0.01 ± 0.01	Correlation
Volume LWP above bankfull channel / m2 - size class 4	V4W_MSQ	0.03 ± 0.03	0.05 ± 0.11	0.01 ± 0.01	0.03 ± 0.08	0.05 ± 0.06	0 ± 0.01	Correlation
Volume LWP above bankfull channel / m2 - size class 5	V5W_MSQ	0.02 ± 0.03	0.03 ± 0.08	0 ± 0	0.02 ± 0.08	0.03 ± 0.06	0 ± 0	0 > 80 %
Number LWP inside + above / m2 - size class 1	C1T_MSQ	0.22 ± 0.17	0.1 ± 0.05	0.12 ± 0.06	0.14 ± 0.05	0.07 ± 0.03	0.06 ± 0.03	Retained
Number LWP inside + above / m2 - size class 2	C2T_MSQ	0.04 ± 0.01	0.05 ± 0.03	0.02 ± 0.02	0.04 ± 0.02	0.04 ± 0.03	0.02 ± 0.01	Correlation
Number LWP inside + above / m2 - size class 3	C3T_MSQ	0.02 ± 0.01	0.02 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0 ± 0	Correlation
Number LWP inside + above / m2 - size class 4	C4T_MSQ	0.01 ± 0	0.01 ± 0.01	0 ± 0	0 ± 0.01	0.01 ± 0	0 ± 0	Correlation
Number LWP inside + above / m2 - size class 5	C5T_MSQ	0 ± 0	0 ± 0.01	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 > 80 %
Volume LWP inside + above / m2 - size class 1	V1T_MSQ	0.07 ± 0.04	0.13 ± 0.18	0.02 ± 0.02	0.06 ± 0.07	0.08 ± 0.07	0.01 ± 0.01	Correlation
Volume LWP inside + above / m2 - size class 2	V2T_MSQ	0.06 ± 0.04	0.12 ± 0.18	0.02 ± 0.02	0.05 ± 0.07	0.08 ± 0.07	0.01 ± 0.01	Correlation
Volume LWP inside + above / m2 - size class 3	V3T_MSQ	0.06 ± 0.04	0.11 ± 0.17	0.02 ± 0.02	0.04 ± 0.07	0.07 ± 0.07	0.01 ± 0.01	Correlation

	Volume LWP inside + above / m2 - size class 4	V4T_MSQ	0.05 ± 0.04	0.1 ± 0.17	0.01 ± 0.01	0.04 ± 0.07	0.06 ± 0.07	0 ± 0.01	Retained
	Volume LWP inside + above / m2 - size class 5	V5T_MSQ	0.03 ± 0.03	0.06 ± 0.13	0 ± 0	0.02 ± 0.08	0.04 ± 0.08	0 ± 0	0 > 80 %
Instream cover for aquatic organisms	Mean large woody fragments (> 0.3 m diameter)	XFC_LWF	27.53 ± 23.03	44.8 ± 31.11	13.14 ± 14.68	4.11 ± 2.03	2.66 ± 2.98	3.34 ± 4.9	Correlation
	Mean small woody fragments (< 0.3 m diameter)	XFC_SWF	41.93 ± 19.56	50.34 ± 27.6	19.11 ± 12.25	22.93 ± 6.39	22.91 ± 10.47	27.92 ± 6.63	Correlation
	Mean trees and roots	XFC_TR	22.81 ± 12.66	47.93 ± 22.38	10.39 ± 7.68	46.86 ± 15.5	12.14 ± 8.78	26.04 ± 9.42	Correlation
	Mean coarse litter	XFC_CL	39.97 ± 22.75	57.16 ± 24.94	43.45 ± 21.4	19.61 ± 10.33	33.7 ± 23.58	17.34 ± 9.57	CAP per block
	Mean overhanging vegetation (up to 1m above channel)	XFC_OV	22.47 ± 9.46	37 ± 16	16.43 ± 7.64	43.36 ± 15.38	18.14 ± 11.19	20.55 ± 13.26	Correlation
	Mean undercut banks	XFC_UB	3.1 ± 2.68	0 ± 0	8.86 ± 5.48	1.14 ± 0.94	2.95 ± 1.38	1.88 ± 1.65	Correlation
	Mean boulder	XFC_BO	1.45 ± 3.58	0 ± 0	0.41 ± 0.73	0 ± 0	5.59 ± 9.01	0 ± 0	Correlation
	Mean natural cover (woody fragments, trees and roots, coarse litter, overhanging vegetation, undercut banks and boulder)	XFC_NAT	159.26 ± 51.95	249.64 ± 109.92	111.8 ± 42.23	160.89 ± 32.03	98.09 ± 42.47	97.08 ± 28.36	Retained

Mean large fish cover (large woody fragments, undercut banks, boulder and artificial structures)	XFC_LAR	32.13 ± 20.59	44.8 ± 31.11	22.41 ± 17.29	5.3 ± 2.55	11.2 ± 10.63	5.55 ± 6.72	Correlation
Proportion of large woody fragments (> 0.3 m diameter)	PFC_LWF	0.8 ± 0.25	0.94 ± 0.12	0.72 ± 0.22	0.36 ± 0.14	0.25 ± 0.22	0.3 ± 0.21	Correlation
Proportion of small woody fragments (< 0.3 m diameter)	PFC_SWF	1 ± 0	0.99 ± 0.03	0.95 ± 0.1	0.98 ± 0.06	0.99 ± 0.03	0.97 ± 0.04	CV
Proportion of trees and roots	PFC_TR	0.92 ± 0.11	1 ± 0	0.88 ± 0.14	1 ± 0	0.93 ± 0.09	0.99 ± 0.03	CV
Proportion of coarse litter	PFC_CL	1 ± 0	1 ± 0	0.99 ± 0.03	0.96 ± 0.08	1 ± 0	0.95 ± 0.09	CV
Proportion of overhanging vegetation (up to 1m above channel)	PFC_OV	1 ± 0	0.99 ± 0.03	0.95 ± 0.08	1 ± 0	0.98 ± 0.04	1 ± 0	CV
Proportion of undercut banks	PFC_UB	0.23 ± 0.24	0 ± 0	0.7 ± 0.22	0.23 ± 0.19	0.48 ± 0.21	0.32 ± 0.27	Retained
Proportion of boulder	PFC_BO	0.08 ± 0.15	0 ± 0	0.08 ± 0.15	0 ± 0	0.22 ± 0.3	0 ± 0	CAP per block
Proportion of natural cover (woody fragments, trees and roots, coarse litter, overhanging vegetation, undercut banks and boulder)	PFC_NAT	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0	CV

	Proportion of large fish cover (large woody fragments, undercut banks, boulder and artificial structures)	PFC_LAR	0.85 ± 0.2	0.94 ± 0.12	0.93 ± 0.07	0.52 ± 0.22	0.67 ± 0.22	0.49 ± 0.23	Retained
Catchment variables	Altitude (m)	Altitude	39.5 ± 9.86	25.1 ± 5.55	119.6 ± 13.47	265.5 ± 70.65	72 ± 12.81	58.71 ± 29.94	Retained
	Catchment slope (%)	Slope	5.55 ± 1.02	6.85 ± 0.59	5.96 ± 1.05	10.23 ± 2.12	11.1 ± 1.1	10.68 ± 3.16	Retained
	Drainage area (Km²)	Drain_Area	2.19 ± 2.38	9.62 ± 10.64	1.57 ± 2.76	11.13 ± 18.24	1.13 ± 1.51	13.02 ± 17.75	Retained
	Mean annual air temperature (ºC)	Temp_Mean	26.83 ± 0.05	26.76 ± 0.05	26.74 ± 0.07	25.28 ± 0.35	27.19 ± 0.09	25.84 ± 0.21	CV
	Temperature of driest quarter (ºC)	Temp_Dry	27.06 ± 0.09	27.27 ± 0.05	26.94 ± 0.07	24.81 ± 0.32	27.78 ± 0.08	26.44 ± 0.21	CV
	Mean annual precipitation (mm)	Prec_Mean	2494.88 ± 26.82	2205.8 ± 27.8	2082.9 ± 55.16	2223.2 ± 11.56	2184.7 ± 6.57	1951.86 ± 55.32	CV
	Precipitation of driest quarter (mm)	Prec_Dry	182.75 ± 16.42	200.7 ± 10.81	81.5 ± 3.75	64.2 ± 0.42	251.8 ± 6.29	149.14 ± 10.25	Correlation
	Proportion of clay in soil (%)	Clay	31.66 ± 1.33	32.84 ± 1.01	33.94 ± 1.61	29.83 ± 0.82	31.94 ± 0.9	36.3 ± 4.5	CV
	Proportion of sand in soil (%)	Sand	47.56 ± 1.32	44.85 ± 2.19	46.19 ± 1.39	45.53 ± 1.76	48.13 ± 1.95	48.79 ± 5.86	CV
	Proportion of coarse fragments in soil (> 2 mm, %)	Coarse fragments	0.17 ± 0.42	0.9 ± 0.34	0.1 ± 0.19	0.18 ± 0.22	0.02 ± 0.04	0.56 ± 0.24	Retained
	Proportion of silt in soil (%)	Silt	20.76 ± 1.00	22.32 ± 1.36	19.71 ± 0.6	24.54 ± 1.56	20.09 ± 1.54	14.93 ± 1.78	Retained

Table S2. Correlations between pairs of local physical habitat variables per block. Bold values indicate strong correlations (r ≥ 0.7). Codes for variables are listed in Table S1.

Channel morphology

	XDEPTH_TR	SDDEPTH_TR	XDEPTH_TH	SDDEPTH_TH	XWIDTH	SDWIDTH	XWXD_P
XDEPTH_TR							
SDDEPTH_TR	**0.84**						
XDEPTH_TH	**0.88**	**0.80**					
SDDEPTH_TH	0.48	0.60	**0.70**				
XWIDTH	0.62	0.62	**0.77**	0.52			
SDWIDTH	0.25	0.19	0.21	0.03	0.52		
XWXD_P	**0.82**	**0.78**	**0.83**	0.46	**0.89**	0.46	
SDWXD_P	0.65	0.69	0.64	0.40	**0.76**	0.63	**0.81**
XWD_RAT_P	-0.47	-0.44	-0.29	-0.23	0.18	0.37	-0.10
SDWD_RAT_P	-0.51	-0.52	-0.42	-0.32	-0.04	0.41	-0.24
XWXD	**0.77**	**0.76**	**0.81**	0.45	**0.89**	0.43	**0.99**
XWD_RAT	-0.32	-0.36	-0.21	-0.22	0.32	0.45	0.04

	SDWXD_P	XWD_RAT_P	SDWD_RAT_P	XWXD
XDEPTH_TR				
SDDEPTH_TR				
XDEPTH_TH				
SDDEPTH_TH				
XWIDTH				
SDWIDTH				
XWXD_P				
SDWXD_P				
XWD_RAT_P	-0.06			
SDWD_RAT_P	-0.19	**0.83**		
XWXD	**0.77**	-0.06	-0.22	
XWD_RAT	0.06	**0.87**	**0.75**	0.05

Substrate

	XEMBED	VEMBED	XCEMBED	VCEMBED	PCT_BIGR	PCT_FG	PCT_SA	PCT_ST	PCT_SFGF
XEMBED									
VEMBED	0.28								
XCEMBED	**0.96**	0.29							
VCEMBED	0.16	**0.94**	0.17						
PCT_BIGR	-0.01	0.14	-0.11	0.22					
PCT_FG	-0.11	0.12	-0.22	0.10	**0.72**				
PCT_SA	0.10	0.31	0.08	0.29	0.12	0.09			
PCT_ST	0.30	-0.21	0.19	-0.27	0.16	0.18	-0.28		
PCT_SFGF	0.37	0.22	0.28	0.14	0.24	0.22	0.59	0.43	
PCT_ORG	-0.37	0.00	-0.25	0.01	-0.60	-0.44	-0.35	-0.32	-0.60
PCT_WD	-0.09	-0.11	-0.05	-0.06	-0.35	-0.35	-0.48	-0.02	-0.48
PCT_HP	-0.12	0.14	-0.18	0.10	0.27	0.52	0.05	0.08	0.10
PCT_RO	-0.03	0.38	0.06	0.39	-0.23	-0.35	0.32	-0.53	0.01
PCT_FL	-0.36	0.03	-0.33	0.04	-0.15	-0.13	-0.20	-0.18	-0.43
PCT_CL	-0.33	-0.10	-0.29	-0.15	-0.34	0.00	-0.25	-0.03	-0.39

	PCT_ORG	PCT_WD	PCT_HP	PCT_RO	PCT_FL
XEMBED					
VEMBED					
XCEMBED					
VCEMBED					
PCT_BIGR					
PCT_FG					
PCT_SA					
PCT_ST					
PCT_SFGF					
PCT_ORG					
PCT_WD	0.36				
PCT_HP	-0.23	-0.39			

PCT_RO	0.33	-0.13	-0.24		
PCT_FL	0.64	0.18	-0.06	0.07	
PCT_CL	0.56	0.08	0.18	-0.25	0.23

Channel habitat units

	PCT_RA	PCT_RI	PCT_GL	PCT_TP	PCT_FAST	PCT_SLOW	PCT_POOL	SEQ_FLO_1
PCT_RA								
PCT_RI	0.36							
PCT_GL	-0.66	-0.54						
PCT_TP	-0.15	-0.09	0.22					
PCT_FAST	0.49	**0.98**	-0.59	-0.11				
PCT_SLOW	-0.64	-0.54	**1.00**	0.27	-0.58			
PCT_POOL	-0.01	-0.12	0.23	**0.78**	-0.09	0.31		
SEQ_FLO_1	-0.07	0.48	0.19	0.40	0.44	0.21	0.38	
SEQ_FLO_2	-0.03	0.60	0.11	0.17	0.55	0.11	0.14	**0.95**

Riparian vegetation cover

	SDCDENMID	SDCDENBANK	XGB	SDGB	XC	SDC	XM
SDCDENMID							
SDCDENBANK	**0.85**						
XGB	0.28	0.36					
SDGB	0.08	0.19	**0.75**				
XC	0.06	0.14	0.10	0.02			
SDC	0.13	0.28	0.16	-0.03	0.12		
XM	0.01	-0.05	0.22	0.09	0.30	-0.13	
SDM	0.11	0.03	-0.12	-0.27	-0.03	0.24	0.01
XG	0.04	0.00	0.35	0.04	0.15	-0.16	0.60
SDG	0.11	0.02	0.02	0.08	0.13	0.10	0.19
XCM	0.03	0.03	0.18	0.06	**0.79**	0.00	**0.82**
SDCM	0.25	0.32	0.01	-0.25	0.14	0.59	0.03
XCMG	0.03	0.01	0.28	0.05	0.62	-0.07	**0.84**
SDCMG	0.24	0.26	0.03	-0.20	0.16	0.44	0.10

	SDM	XG	SDG	XCM	SDCM	XCMG
SDCDENMID						
SDCDENBANK						
XGB						
SDGB						
XC						
SDC						
XM						
SDM						
XG	-0.18					
SDG	0.16	-0.08				
XCM	0.00	0.46	0.21			
SDCM	0.68	-0.10	0.20	0.11		
XCMG	-0.07	**0.79**	0.09	**0.91**	0.03	

SDCMG	0.54	-0.05	0.45	0.16	**0.80**	0.09

Large woody pieces

	C1W_100	C2W_100	C3W_100	C4W_100	V1W_100	V2W_100	V3W_100	V4W_100	C1D_100	C2D_100	C3D_100
C1W_100											
C2W_100	0.51										
C3W_100	0.33	**0.78**									
C4W_100	0.27	0.63	**0.81**								
V1W_100	0.51	**0.80**	**0.86**	**0.85**							
V2W_100	0.32	**0.75**	**0.89**	**0.87**	**0.96**						
V3W_100	0.29	**0.74**	**0.89**	**0.86**	**0.94**	**0.93**					
V4W_100	0.23	0.58	**0.76**	**0.94**	**0.89**	**0.91**	**0.91**				
C1D_100	0.35	0.09	0.20	0.10	0.20	0.11	0.19	0.12			
C2D_100	0.03	0.37	0.47	0.41	0.43	0.45	0.49	0.44	0.56		
C3D_100	-0.11	0.28	0.47	0.39	0.37	0.39	0.47	0.40	0.49	**0.84**	
C4D_100	-0.17	0.28	0.48	0.46	0.42	0.48	0.52	0.47	0.24	0.56	**0.72**
V1W_100	-0.05	0.27	0.46	0.43	0.45	0.48	0.53	0.50	0.45	0.69	**0.77**
V2W_100	-0.07	0.28	0.47	0.44	0.46	0.49	0.54	0.50	0.41	**0.70**	**0.78**
V3W_100	-0.09	0.26	0.45	0.43	0.44	0.47	0.52	0.49	0.39	0.66	**0.78**
V4W_100	-0.13	0.22	0.40	0.40	0.39	0.44	0.48	0.45	0.26	0.49	0.62
C1T_100	**0.94**	0.47	0.34	0.26	0.48	0.30	0.28	0.22	0.58	0.19	0.05
C2T_100	0.34	**0.89**	**0.76**	0.62	**0.75**	**0.74**	**0.73**	0.58	0.26	**0.71**	0.57
C3T_100	0.12	0.61	**0.85**	0.68	0.69	**0.72**	**0.77**	0.65	0.40	**0.77**	**0.85**
C4T_100	0.03	0.53	**0.76**	**0.81**	**0.71**	**0.77**	**0.79**	**0.79**	0.21	0.60	0.68
V1T_100	0.21	0.60	**0.74**	**0.71**	**0.80**	**0.80**	**0.81**	**0.76**	0.36	0.64	0.66
V2T_100	0.12	0.61	**0.74**	**0.70**	**0.77**	**0.79**	**0.81**	**0.75**	0.29	0.68	0.69
V3T_100	0.06	0.50	**0.73**	0.69	**0.71**	**0.75**	**0.79**	**0.74**	0.33	0.68	**0.73**
V4T_100	0.00	0.44	0.66	**0.71**	0.67	**0.72**	**0.75**	**0.76**	0.24	0.57	0.63
C1W_MSQ	**0.71**	0.06	-0.01	-0.04	0.16	-0.03	-0.01	-0.03	0.61	0.15	0.07
C2W_MSQ	0.33	**0.79**	**0.72**	0.59	**0.71**	0.67	**0.70**	0.57	0.26	0.53	0.50
C3W_MSQ	0.19	0.63	**0.90**	**0.78**	**0.78**	**0.82**	**0.83**	**0.74**	0.25	0.52	0.59
C4W_MSQ	0.15	0.47	0.69	**0.89**	**0.77**	**0.79**	**0.79**	**0.87**	0.14	0.41	0.45
V1W_MSQ	0.14	0.43	0.60	**0.70**	**0.79**	**0.78**	**0.79**	**0.82**	0.21	0.44	0.47
V2W_MSQ	0.06	0.41	0.59	**0.71**	**0.77**	**0.79**	**0.77**	**0.83**	0.14	0.42	0.45

V3W_MSQ	0.05	0.41	0.60	**0.71**	**0.77**	**0.77**	**0.80**	**0.83**	0.15	0.42	0.48
V4W_MSQ	0.02	0.32	0.50	0.68	**0.71**	**0.73**	**0.73**	**0.81**	0.10	0.35	0.40
C1D_MSQ	0.16	-0.19	-0.10	-0.16	-0.06	-0.13	-0.09	-0.10	**0.83**	0.46	0.44
C2D_MSQ	-0.18	0.02	0.12	0.07	0.11	0.15	0.16	0.15	0.52	**0.82**	**0.73**
C3D_MSQ	-0.30	0.01	0.18	0.12	0.10	0.15	0.19	0.15	0.41	0.69	**0.85**
C4D_MSQ	-0.25	0.07	0.29	0.29	0.28	0.34	0.35	0.34	0.29	0.52	0.66
V1W_MSQ	-0.15	0.04	0.19	0.25	0.29	0.31	0.31	0.34	0.27	0.40	0.50
V2W_MSQ	-0.16	0.04	0.19	0.26	0.29	0.32	0.31	0.35	0.26	0.40	0.50
V3W_MSQ	-0.16	0.03	0.19	0.25	0.28	0.31	0.30	0.34	0.25	0.38	0.49
V4W_MSQ	-0.15	0.02	0.16	0.25	0.27	0.30	0.29	0.33	0.21	0.32	0.41
C1T_MSQ	0.62	-0.01	-0.03	-0.07	0.11	-0.06	-0.03	-0.05	**0.71**	0.24	0.17
C2T_MSQ	0.11	0.54	0.55	0.44	0.53	0.53	0.56	0.46	0.47	**0.82**	**0.74**
C3T_MSQ	-0.10	0.34	0.60	0.49	0.48	0.54	0.57	0.49	0.41	**0.74**	**0.88**
C4T_MSQ	-0.11	0.27	0.52	0.61	0.55	0.60	0.61	0.63	0.26	0.55	0.67
V1T_MSQ	-0.04	0.22	0.39	0.48	0.55	0.56	0.56	0.60	0.28	0.48	0.56
V2T_MSQ	-0.07	0.23	0.40	0.49	0.55	0.57	0.57	0.61	0.25	0.47	0.56
V3T_MSQ	-0.09	0.20	0.39	0.48	0.52	0.55	0.55	0.60	0.23	0.45	0.54
V4T_MSQ	-0.09	0.15	0.33	0.46	0.49	0.51	0.51	0.57	0.19	0.38	0.47

	C4D_100	V1W_100	V2W_100	V3W_100	V4W_100	C1T_100	C2T_100	C3T_100	C4T_100	V1T_100	V2T_100
C1W_100											
C2W_100											
C3W_100											
C4W_100											
V1W_100											
V2W_100											
V3W_100											
V4W_100											
C1D_100											
C2D_100											
C3D_100											
C4D_100											

V1W_100	**0.85**										
V2W_100	**0.85**	**1.00**									
V3W_100	**0.87**	**0.99**	**1.00**								
V4W_100	**0.91**	**0.94**	**0.94**	**0.95**							
C1T_100	-0.06	0.08	0.06	0.04	-0.03						
C2T_100	0.45	0.48	0.50	0.46	0.36	0.40					
C3T_100	0.68	**0.70**	**0.71**	**0.70**	0.57	0.23	**0.79**				
C4T_100	**0.87**	**0.77**	**0.78**	**0.78**	**0.79**	0.10	0.64	**0.82**			
V1T_100	**0.75**	**0.87**	**0.87**	**0.86**	**0.81**	0.30	**0.72**	**0.81**	**0.88**		
V2T_100	**0.78**	**0.87**	**0.88**	**0.87**	**0.82**	0.20	**0.75**	**0.83**	**0.89**	**0.99**	
V3T_100	**0.80**	**0.90**	**0.91**	**0.90**	**0.85**	0.15	0.65	**0.85**	**0.91**	**0.97**	**0.98**
V4T_100	**0.82**	**0.88**	**0.88**	**0.88**	**0.88**	0.08	0.56	**0.73**	**0.93**	**0.93**	**0.95**
C1W_MSQ	-0.10	0.07	0.04	0.03	-0.05	**0.79**	0.07	0.03	-0.10	0.10	0.01
C2W_MSQ	0.35	0.39	0.40	0.37	0.27	0.34	**0.78**	0.67	0.55	0.60	0.61
C3W_MSQ	0.57	0.53	0.54	0.53	0.45	0.22	0.66	**0.82**	**0.77**	**0.73**	**0.73**
C4W_MSQ	0.53	0.49	0.49	0.48	0.46	0.15	0.49	0.62	**0.77**	0.69	0.67
V1W_MSQ	0.50	0.55	0.55	0.53	0.47	0.16	0.47	0.57	0.65	**0.72**	0.69
V2W_MSQ	0.50	0.53	0.53	0.52	0.46	0.07	0.45	0.56	0.66	**0.70**	0.68
V3W_MSQ	0.53	0.55	0.55	0.54	0.49	0.06	0.45	0.57	0.67	**0.72**	**0.70**
V4W_MSQ	0.47	0.50	0.50	0.49	0.45	0.02	0.36	0.48	0.62	0.65	0.63
C1D_MSQ	0.21	0.39	0.36	0.35	0.25	0.37	0.03	0.19	0.05	0.18	0.13
C2D_MSQ	0.48	0.57	0.57	0.54	0.42	0.01	0.38	0.50	0.36	0.40	0.42
C3D_MSQ	0.62	0.62	0.62	0.63	0.51	-0.11	0.33	0.60	0.47	0.44	0.46
C4D_MSQ	**0.90**	**0.78**	**0.78**	**0.78**	**0.81**	-0.11	0.28	0.52	**0.71**	0.64	0.65
V1W_MSQ	**0.71**	**0.82**	**0.81**	**0.81**	**0.81**	-0.05	0.18	0.37	0.57	0.69	0.67
V2W_MSQ	**0.72**	**0.82**	**0.81**	**0.81**	**0.81**	-0.06	0.18	0.37	0.57	0.69	0.68
V3W_MSQ	**0.71**	**0.81**	**0.80**	**0.80**	**0.81**	-0.07	0.17	0.37	0.57	0.68	0.67
V4W_MSQ	0.69	**0.78**	**0.77**	**0.77**	**0.80**	-0.07	0.13	0.31	0.55	0.65	0.64
C1T_MSQ	-0.03	0.16	0.13	0.11	0.02	**0.74**	0.06	0.07	-0.07	0.13	0.04
C2T_MSQ	0.50	0.58	0.59	0.55	0.41	0.23	**0.73**	**0.73**	0.56	0.63	0.64
C3T_MSQ	**0.71**	0.69	**0.70**	**0.70**	0.58	0.04	0.57	**0.83**	**0.72**	0.68	**0.69**
C4T_MSQ	**0.87**	**0.77**	**0.77**	**0.77**	**0.77**	-0.01	0.42	0.65	0.85	**0.76**	**0.76**

V1T_MSQ	**0.71**	**0.81**	**0.80**	**0.79**	**0.77**	0.04	0.33	0.51	0.68	**0.80**	**0.77**
V2T_MSQ	**0.72**	**0.81**	**0.80**	**0.79**	**0.77**	0.00	0.34	0.52	0.69	**0.80**	**0.78**
V3T_MSQ	**0.72**	**0.80**	**0.80**	**0.79**	**0.77**	-0.02	0.31	0.50	0.69	**0.78**	**0.77**
V4T_MSQ	0.69	**0.77**	**0.76**	**0.76**	**0.76**	-0.04	0.25	0.42	0.65	**0.75**	**0.73**

	V3T_100	V4T_100	C1W_MSQ	C2W_MSQ	C3W_MSQ	C4W_MSQ	V1W_MSQ	V2W_MSQ	V3W_MSQ	V4W_MSQ	C1D_MSQ
C1W_100											
C2W_100											
C3W_100											
C4W_100											
V1W_100											
V2W_100											
V3W_100											
V4W_100											
C1D_100											
C2D_100											
C3D_100											
C4D_100											
V1W_100											
V2W_100											
V3W_100											
V4W_100											
C1T_100											
C2T_100											
C3T_100											
C4T_100											
V1T_100											
V2T_100											
V3T_100											
V4T_100	**0.96**										
C1W_MSQ	0.00	-0.07									
C2W_MSQ	0.55	0.48	0.16								

C3W_MSQ	**0.73**	0.67	0.03	**0.80**							
C4W_MSQ	0.67	0.68	0.00	0.59	**0.83**						
V1W_MSQ	0.68	0.66	0.08	0.61	**0.76**	**0.86**					
V2W_MSQ	0.67	0.66	-0.04	0.58	**0.76**	**0.86**	**0.99**				
V3W_MSQ	0.68	0.67	-0.03	0.57	**0.76**	**0.86**	**0.99**	**0.99**			
V4W_MSQ	0.62	0.63	-0.05	0.46	0.67	**0.85**	**0.98**	**0.98**	**0.99**		
C1D_MSQ	0.18	0.11	0.66	0.07	0.05	-0.03	0.10	0.02	0.03	0.00	
C2D_MSQ	0.44	0.36	0.16	0.33	0.31	0.21	0.33	0.31	0.30	0.26	0.67
C3D_MSQ	0.50	0.43	0.04	0.33	0.39	0.28	0.35	0.33	0.35	0.30	0.54
C4D_MSQ	0.67	0.69	-0.05	0.23	0.46	0.48	0.54	0.54	0.56	0.53	0.35
V1W_MSQ	0.68	**0.70**	0.03	0.20	0.36	0.46	0.58	0.57	0.58	0.58	0.33
V2W_MSQ	0.69	**0.70**	0.02	0.20	0.36	0.46	0.58	0.58	0.59	0.59	0.32
V3W_MSQ	0.68	**0.70**	0.02	0.18	0.35	0.46	0.57	0.56	0.58	0.58	0.30
V4W_MSQ	0.65	0.68	0.01	0.13	0.31	0.45	0.54	0.54	0.55	0.57	0.26
C1T_MSQ	0.05	-0.03	**0.98**	0.15	0.04	0.00	0.09	-0.03	-0.02	-0.04	**0.79**
C2T_MSQ	0.61	0.52	0.20	**0.84**	**0.70**	0.51	0.59	0.56	0.55	0.45	0.43
C3T_MSQ	**0.72**	0.64	0.04	0.64	**0.79**	0.62	0.63	0.62	0.63	0.55	0.39
C4T_MSQ	**0.78**	**0.79**	-0.03	0.43	**0.70**	**0.79**	**0.77**	**0.77**	**0.78**	**0.76**	0.23
V1T_MSQ	**0.78**	**0.78**	0.06	0.41	0.58	0.68	**0.83**	**0.82**	**0.83**	**0.82**	0.27
V2T_MSQ	**0.78**	**0.79**	0.01	0.41	0.59	0.69	**0.83**	**0.83**	**0.83**	**0.82**	0.23
V3T_MSQ	**0.77**	**0.78**	0.00	0.37	0.57	0.68	**0.82**	**0.81**	**0.82**	**0.82**	0.22
V4T_MSQ	**0.73**	**0.76**	-0.01	0.29	0.50	0.66	**0.79**	**0.79**	**0.80**	**0.81**	0.19

	C2D_MSQ	C3D_MSQ	C4D_MSQ	V1W_MSQ	V2W_MSQ	V3W_MSQ	V4W_MSQ	C1T_MSQ	C2T_MSQ	C3T_MSQ	C4T_MSQ
C1W_100											
C2W_100											
C3W_100											
C4W_100											
V1W_100											
V2W_100											
V3W_100											
V4W_100											

C1D_100						
C2D_100						
C3D_100						
C4D_100						
V1W_100						
V2W_100						
V3W_100						
V4W_100						
C1T_100						
C2T_100						
C3T_100						
C4T_100						
V1T_100						
V2T_100						
V3T_100						
V4T_100						
C1W_MSQ						
C2W_MSQ						
C3W_MSQ						
C4W_MSQ						
V1W_MSQ						
V2W_MSQ						
V3W_MSQ						
V4W_MSQ						
C1D_MSQ						
C2D_MSQ						
C3D_MSQ	**0.83**					
C4D_MSQ	0.59	**0.73**				
V1W_MSQ	0.46	0.53	**0.85**			
V2W_MSQ	0.46	0.53	**0.85**	**1.00**		
V3W_MSQ	0.43	0.53	**0.84**	**1.00**	**1.00**	
V4W_MSQ	0.36	0.44	**0.82**	**0.99**	**0.99**	**0.99**

C1T_MSQ	0.30	0.17	0.05	0.11	0.10	0.09	0.07				
C2T_MSQ	**0.78**	**0.69**	0.49	0.39	0.39	0.36	0.29	0.27			
C3T_MSQ	**0.72**	**0.87**	**0.73**	0.54	0.55	0.54	0.46	0.13	**0.83**		
C4T_MSQ	0.51	0.63	**0.92**	**0.80**	**0.80**	**0.79**	**0.77**	0.03	0.57	**0.79**	
V1T_MSQ	0.46	0.52	**0.81**	**0.94**	**0.94**	**0.93**	**0.91**	0.12	0.53	0.65	**0.87**
V2T_MSQ	0.46	0.52	**0.81**	**0.93**	**0.93**	**0.93**	**0.91**	0.07	0.53	0.66	**0.88**
V3T_MSQ	0.43	0.51	**0.81**	**0.94**	**0.94**	**0.94**	**0.92**	0.05	0.49	0.64	**0.88**
V4T_MSQ	0.37	0.43	**0.79**	**0.94**	**0.95**	**0.94**	**0.94**	0.04	0.40	0.55	**0.86**

	V1T_MSQ	V2T_MSQ	V3T_MSQ
C1W_100			
C2W_100			
C3W_100			
C4W_100			
V1W_100			
V2W_100			
V3W_100			
V4W_100			
C1D_100			
C2D_100			
C3D_100			
C4D_100			
V1W_100			
V2W_100			
V3W_100			
V4W_100			
C1T_100			
C2T_100			
C3T_100			
C4T_100			
V1T_100			
V2T_100			

V3T_100			
V4T_100			
C1W_MSQ			
C2W_MSQ			
C3W_MSQ			
C4W_MSQ			
V1W_MSQ			
V2W_MSQ			
V3W_MSQ			
V4W_MSQ			
C1D_MSQ			
C2D_MSQ			
C3D_MSQ			
C4D_MSQ			
V1W_MSQ			
V2W_MSQ			
V3W_MSQ			
V4W_MSQ			
C1T_MSQ			
C2T_MSQ			
C3T_MSQ			
C4T_MSQ			
V1T_MSQ			
V2T_MSQ	**1.00**		
V3T_MSQ	**1.00**	**1.00**	
V4T_MSQ	**0.98**	**0.99**	**0.99**

Instream cover for aquatic organisms

	XFC_LWF	XFC_SWF	XFC_TR	XFC_CL	XFC_OV	XFC_UB	XFC_BO	XFC_NAT	XFC_LAR	PFC_LWF	PFC_UB	PFC_BO
XFC_LWF												
XFC_SWF	0.63											
XFC_TR	0.27	0.52										
XFC_CL	0.37	0.26	0.06									
XFC_OV	0.28	0.36	**0.71**	0.15								
XFC_UB	-0.22	-0.34	-0.59	-0.14	-0.47							
XFC_BO	-0.11	-0.14	-0.35	-0.21	-0.22	0.19						
XFC_NAT	0.67	**0.75**	**0.73**	0.53	**0.71**	-0.49	-0.28					
XFC_LAR	**0.90**	0.55	0.02	0.34	0.06	0.04	0.18	0.49				
PFC_LWF	**0.87**	0.42	0.16	0.41	0.31	-0.19	-0.06	0.56	**0.76**			
PFC_UB	-0.34	-0.43	-0.64	-0.18	-0.43	**0.85**	0.24	-0.53	-0.07	-0.24		
PFC_BO	-0.13	-0.21	-0.41	-0.15	-0.27	0.22	**0.94**	-0.30	0.16	-0.08	0.30	
PFC_LAR	0.60	0.20	-0.19	0.38	0.03	0.10	0.22	0.28	**0.73**	**0.77**	0.21	0.26

After CAP per block

	SDDEPTH_TH	PCT_WD	PCT_RO	PCT_ST	PCT_SFGF	PCT_RA	PCT_FAST
SDDEPTH_TH							
PCT_WD	0.06						
PCT_RO	-0.01	-0.13					
PCT_ST	-0.26	-0.02	-0.53				
PCT_SFGF	-0.12	-0.48	0.01	0.43			
PCT_RA	0.16	-0.30	0.15	-0.11	0.30		
PCT_FAST	0.05	-0.41	0.34	-0.23	0.42	0.49	
SDCDENBANK	0.33	-0.26	-0.04	-0.05	0.06	0.37	0.19
SDGB	0.06	-0.24	-0.01	0.10	0.35	0.17	0.17
XCMG	0.19	0.14	0.29	-0.14	-0.08	0.00	0.05
XFC_NAT	0.23	0.35	0.19	-0.08	-0.43	-0.32	-0.41
PFC_UB	0.01	-0.32	-0.14	0.14	0.35	0.06	0.37
PFC_LAR	0.18	0.24	-0.37	0.30	-0.20	-0.37	-0.36
C1T_MSQ	0.08	0.18	0.17	-0.15	0.05	-0.26	-0.02
V4T_MSQ	-0.09	0.09	-0.31	0.30	0.13	-0.18	-0.09

	SDCDENBANK	SDGB	XCMG	XFC_NAT	PFC_UB	PFC_LAR	C1T_MSQ
SDDEPTH_TH							
PCT_WD							
PCT_RO							
PCT_ST							
PCT_SFGF							
PCT_RA							
PCT_FAST							
SDCDENBANK							
SDGB	0.19						
XCMG	0.01	0.05					
XFC_NAT	-0.21	-0.32	0.26				
PFC_UB	0.15	0.49	-0.14	-0.53			

PFC_LAR	-0.20	-0.06	-0.27	0.28	0.21		
C1T_MSQ	-0.29	0.06	-0.11	0.16	0.02	0.11	
V4T_MSQ	-0.28	-0.19	0.08	0.09	-0.14	0.21	0.04

Table S3. Results of PERMANOVA pairwise analysis.

	Pairs	**t**	**p**
Local scale	Acará, Anapu	2.857	**<0.001**
	Acará, Capim	0.974	0.429
	Acará, Negro	2.760	**0.001**
	Acará, Juruena	2.277	**0.002**
	Acará, Tapajós	1.835	**0.023**
	Anapu, Capim	3.197	**<0.001**
	Anapu, Negro	4.900	**<0.001**
	Anapu, Juruena	4.220	**<0.001**
	Anapu, Tapajós	3.620	**<0.001**
	Capim, Negro	3.236	**<0.001**
	Capim, Juruena	2.215	**0.001**
	Capim, Tapajós	2.104	**0.004**
	Negro, Juruena	4.148	**<0.001**
	Negro, Tapajós	2.595	**<0.001**
	Juruena, Tapajós	1.883	**0.018**
Catchment scale	Acará, Anapu	4.529	**<0.001**
	Acará, Capim	5.099	**<0.001**
	Acará, Negro	6.748	**<0.001**
	Acará, Juruena	6.131	**<0.001**
	Acará, Tapajós	4.695	**<0.001**
	Anapu, Capim	5.564	**<0.001**
	Anapu, Negro	5.218	**<0.001**
	Anapu, Juruena	5.433	**<0.001**
	Anapu, Tapajós	2.506	**0.002**
	Capim, Negro	6.929	**<0.001**
	Capim, Juruena	3.120	**<0.001**
	Capim, Tapajós	3.721	**<0.001**
	Negro, Juruena	5.691	**<0.001**
	Negro, Tapajós	3.559	**<0.001**
	Juruena, Tapajós	2.950	**0.001**

Table S4. Results of PERMDISP pairwise analysis.

	Pairs	**t**	**p**
Local scale	Acará, Anapu	1.677	0.150
	Acará, Capim	0.124	0.930
	Acará, Negro	1.389	0.300
	Acará, Juruena	0.442	0.726
	Acará, Tapajós	0.279	0.874
	Anapu, Capim	2.627	**0.019**
	Anapu, Negro	3.970	**0.001**
	Anapu, Juruena	1.794	0.110
	Anapu, Tapajós	1.376	0.217
	Capim, Negro	2.455	**0.032**
	Capim, Juruena	1.009	0.345
	Capim, Tapajós	0.573	0.785
	Negro, Juruena	2.966	**0.013**
	Negro, Tapajós	1.894	0.115
	Juruena, Tapajós	0.067	0.965
Catchment scale	Acará, Anapu	0.911	0.499
	Acará, Capim	1.366	0.254
	Acará, Negro	0.715	0.513
	Acará, Juruena	3.727	**0.006**
	Acará, Tapajós	2.210	**0.034**
	Anapu, Capim	0.144	0.899
	Anapu, Negro	1.555	0.203
	Anapu, Juruena	2.736	**0.015**
	Anapu, Tapajós	1.268	0.299
	Capim, Negro	2.146	0.050
	Capim, Juruena	2.995	**0.020**
	Capim, Tapajós	1.379	0.183
	Negro, Juruena	4.548	**0.001**
	Negro, Tapajós	2.860	**0.009**
	Juruena, Tapajós	1.159	0.280

Capítulo 2

Partitioning taxonomic and functional diversity of Amazon stream fish between environment and space

O capítulo II desta tese foi elaborado e formatado conforme as normas da publicação científica *Global Ecology and Biogeography*, as quais se encontram em anexo (Anexo 2)

Partitioning taxonomic and functional diversity of Amazon stream fish between environment and space

Running title: Partitioning Amazon stream fish diversity

Abstract

Aim: Environmental filtering and dispersal limitations are essential processes affecting the variability of stream fish. However, the relative role of environmental and spatial variables in organising fish assemblages is highly debated, and remains largely unknown in the Amazon Basin. We aimed to determine what is the relative role of spatial and catchment and local variables on taxonomic and functional alpha and beta diversity of stream fish.

Location: 54 streams across six river basins in the Amazon.

Time period: 2012 – 2015.

Major taxa studied: Fish.

Methods: In each stream, we selected a 150-m reach to collect fish specimens and measure 35 local physical habitat variables. We extracted 11 catchment variables and fluvial distance among all streams through GIS data. Fish were sampled with hand nets. After reducing the number of variables through forward selection, we visualized their effect on fish assemblages with RDA analysis. We partitioned variation with partial RDA.

Results: We found that taxonomic and functional alpha diversities are affected by local and spatial variables, with no influence from catchment variables. Conversely, taxonomic and functional beta diversities are strongly affected by catchment and spatial variables.

Main conclusions: Spatial variables are proxies of dispersal limitation, accounting for the strong biogeographical effects in fish assemblages. Regarding environment, altitude and slope are the main drivers of variation, regulating local conditions and species turnover. Our results clearly show the need of including environmental and spatial variables in studies of stream fish, as they are related to distinct processes regulating fish assemblages. We encourage future studies to account for the responses of multiple facets of biodiversity to different drivers, as they provide essential complementary informations for biodiversity conservation.

Keywords: dispersal; environmental filtering; variation partitioning; alpha diversity; beta diversity; stream fish.

Introduction

One of the main goals of community ecology is to describe patterns of species distribution in space and to unveil its underlying drivers (Clarke, Mac Nally, Bond, & Lake, 2010; Sharma, Legendre, De Cáceres, & Boisclair, 2011). The decomposition of regional diversity (i.e. gamma diversity) into alpha (i.e. within-community) and beta (i.e. among-communities) components allows assessing community structure and the distinct processes linked to each component (Clarke et al., 2010; De Bello, Lavergne, Meynard, Lepš, & Thuiller, 2010; Mokany, Harwood, Overton, Barker, & Ferrier, 2011; Zbinden & Matthews, 2017). In stream ecology, alpha (α) and beta (β) diversity have been shown to be strongly related to environment selection and dispersal limitation (Blanchet, Helmus, Brosse, & Grenouillet, 2014; Sály, Takács, Kiss, Bíró, & Erős, 2011; Sharma et al., 2011; Zbinden & Matthews, 2017).

Physical habitat variables such as width, substrate and canopy cover are correlated with species richness and relative abundance (Leitão, Zuanon, Mouillot, Leal, Hughes, et al., 2017; Mendonça, Magnusson, & Zuanon, 2005; Pease, Taylor, Winemiller, & King, 2011). However, because streams are nested within a fluvial hierarchy, these local variables are directly shaped by large-scale variables acting within the catchment, such as geology, climate, and vegetation (Benone, Esposito, Juen, Pompeu, & Montag, 2017; Frissell, Liss, Warren, & Hurley, 1986; Grabowski, Surian, & Gurnell, 2014; Leal et al., 2016). These large-scale variables are responsible for the main features of streams within a catchment, leading to dissimilarities in fish assemblages' structure among and within river basins (Hoeinghaus, Winemiller, & Birnbaum, 2007; Wang et al., 2003). Thus, diversity patterns of stream fish are determined by multiple environmental factors operating at different spatial scales (Macedo et al., 2014; Paller et al., 2016; Wang et al., 2003).

Variation of abiotic factors in space can lead to clumped patterns of species distribution (e.g. Heino & Tolonen, 2017; Hoeinghaus et al., 2007; Paller et al., 2016), where species are substituted along a gradient of spatially structured environmental variables (Carvalho & Tejerina-Garro, 2015; Pease, Taylor, Winemiller, & King, 2015). However, patterns in fish spatial distribution can also arise from dispersal limitation (Sharma et al., 2011), where stream size and proximity are usual constraints (Hitt & Angermeier, 2008). Thus, community similarity is expected to decrease with spatial distance due to isolation, physical barriers, and changes in the environmental gradient.

Taxonomic and functional diversity of fishes can respond to environmental drivers in different ways (Hoeinghaus et al., 2007; Macedo et al., 2014; Paller et al., 2016; Pease et al., 2011, 2015). Taxonomic diversity has been attributed to large-scale processes and variables controlling the regional species pool, such as dispersal (Hitt & Angermeier, 2008), historical factors (Oberdorff et al., 2011), topography (Macedo et al., 2014), and climate (Buisson, Thuiller, Lek, Lim, & Grenouillet, 2008). In contrast, functional traits should reflect species' adaptations to local environmental conditions, which can lead to major changes in functional composition (Carvalho & Tejerina-Garro, 2015; Göthe et al., 2017; Oliveira et al., 2012; Ribeiro, Teresa, & Casatti, 2016). Studies comparing the effects of environmental variables on taxonomic and functional diversity show varying responses, with either similar (Paller et al., 2016; Terra, Hughes, & Araújo, 2016) or dissimilar influence of catchment and local variables (Hoeinghaus et al., 2007; Pease et al., 2011; Wang et al., 2003). This lack of congruency indicates that more work on taxonomic and functional responses of fish assemblages to environmental variables is needed.

The study of undisturbed streams could improve understanding of the relative importance of spatial and environmental variables affecting fish assemblages (Wang et al., 2003; Wang, Seelbach, & Lyons, 2006). In the Amazon Basin, In the Amazon Basin, undisturbed streams within large remote areas provide an opportunity to examine relationships between natural environmental variation and taxonomic and functional diversity of aquatic organisms. Most studies of Amazonian stream fishes have focused on relationships of local environmental variables on taxonomic diversity (e. g. Espírito-Santo et al., 2009; Mendonça et al., 2005; Prudente, Pompeu, Juen, & Montag, 2017), and few have considered potential influences of large-scale variables (Fernandes, Lourenço, Ota, Moreira, & Zawadzki, 2013). Even fewer studies have examined fish functional traits in relation to environmental variables at multiple scales (Cilleros, Allard, Grenouillet, & Brosse, 2016; Leitão et al., 2017).

We used data from stream fish assemblages across six river basins in the Amazon to address the following question: what is the relative role of spatial and environmental variables in different scales on alpha and beta diversity of Amazon stream fish based on either taxonomic or functional measures of diversity? We predict a stronger association between local physical habitat variables with functional alpha and beta diversity, whereas taxonomic alpha and beta diversity should be more strongly associated with spatial and catchment variables.

Material and Methods

Study area

We sampled 54 1st to 4th order streams distributed in six river basins: Acará (10 streams), Anapu (10), Capim (10), Juruena (7), Negro (10) and Tapajós (7) River Basins (Figure 1). All streams drain well preserved areas under legal protection, four in public land and two (Acará and Capim) in private areas. Watersheds of the six river basins are mostly covered by rain forest (Barthem, Charvet-Almeida, Montag, & Lanna, 2004). More details can be found in Benone et al. (2017).

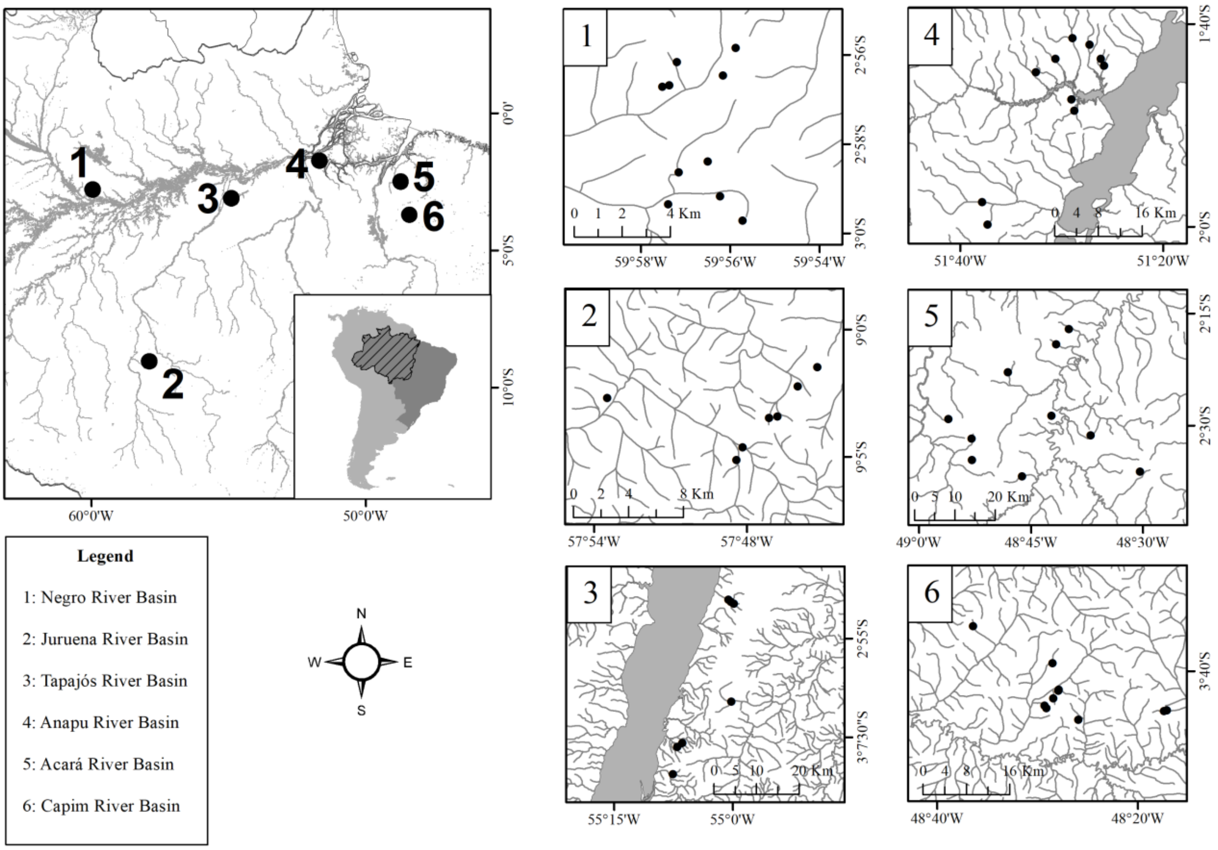

Figure 1. Location of the 54 sampled streams, distributed in six river basins across the Amazon.

Local physical habitat variables

In each stream, we defined a 150-m long stretch that was then divided by 11 cross-sections yielding 10 longitudinal sections of 15 m. We applied the physical habitat assessment protocol for wadeable streams of the U. S. Environmental Protection Agency (US-EMAP, Kaufmann, Levine, Peck, Robison, & Seeliger, 1999; Peck et al., 2006). We sampled during the dry season when the protocol is more efficient (Peck et al., 2006). We measured 35 physical habitat variables divided in six blocks (Appenxdix S1 in the Supporting information): channel morphology (e.g. width, depth), substrate (e.g. bedrock, sand), channel habitat units (e.g. riffle, pool), riparian vegetation cover (e.g canopy cover), large woody fragments (> 1.5 m long and > 10 cm at the smaller end diameter), and instream cover for aquatic organisms (e.g. coarse and fine litter). Details of the physical habitat assessment are provided in the Supporting information.

Catchment variables

We defined 11 catchment variables (Appendix S2) that described conditions in the upstream drainage areas of each sample site: mean annual air temperature (ºC), temperature of the driest quarter (ºC), mean annual precipitation (mm), precipitation of the driest quarter (mm), altitude (m), catchment slope (%), drainage area (km²), and proportion of coarse fragments (> 2 mm, %), clay (%), sand (%) and silt (%) in soil. Temperature and precipitation were obtained from BioClim (http://www.worldclim.org/bioclim). We calculated altitude, catchment slope, and drainage area using Shuttle Radar Topography Mission (SRTM) images, obtained at EarthExplorer, and the ArcHydro tool with ArcGis software. (http://earthexplorer.usgs.gov/). Soil data at 0-cm depth were obtained at SoilsGrid1km (http://soilgrids1km.isric.org/). We calculated the proportion for each soil variable using Spatial Analyst tool with ArcGIS software.

Spatial variables

We obtained fluvial distances (following the contours of streams) between all pairs of streams using ArcHydro tool and Network Analyst tool within ArcGIS software. The shapes of the local drainage system at 1:100,000 scale were used to calculate these distances. We used a former calculation of Moran's Eigenvector Maps (MEM), known as principal coordinates of neighbour matrices (PCNM, Dray, Legendre, & Peres-Neto, 2006) in the fluvial distance matrix to obtain the spatial arrangement of streams. The resulting variables represent the spatial structure, which is related to the spatial autocorrelation of biotic and abiotic factors (Dray et al., 2006). We used the R package *PCNM* (Legendre, Borcard, Blanchet, & Dray, 2013) to obtain the spatial variables, selecting only those with Moran's I > 1 and $p < 0.05$.

Fish sampling

Fish specimens were collected using 55-cm diameter hand nets with 2-mm mesh during a six-hour period. This period was divided equally according to the ten longitudinal sections and the number of collectors. Fishes were euthanized with lethal doses of anesthesia (Leary et al., 2013), fixed in 10% formalin, and after 48 h, preserved in 70% alcohol. Specimens were identified to the lowest possible taxonomic level using identification keys in literature complemented by guidance from ichthological specialists. Voucher specimens were deposited in the ichthyological collection of Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil.

Functional traits

We obtained functional traits from five individuals of similar size of each species. For species with sexual dimorphism, we selected only female individuals (Ribeiro et al., 2016). Quantitative traits were chosen based on 16 morphological measures: standard length (SL), maximum body height (MBH), maximum body width (MBW), length of caudal peduncle (LCP), maximum height of caudal peduncle (MHCP), maximum width of caudal peduncle (MWCP), length of pectoral fin (LPF), height of pectoral fin (HPF), height of body midline (HBM), height of eye midline (HEM), head length (HL), head height (HH), mouth width (MW), body area (BA), pectoral fin area (PFA), and mouth orientation (MO) (Ohlberger, Staaks, & Hölker, 2006; Watson & Balon, 1984).

All measures were taken with a digital caliper with 0.1 mm of precision. Areas of the body and fins were estimated with ImageJ software based on outline drawings. These 16 measures were used to obtain 12 ecomorphological indices (Ohlberger, Staaks, & Hölker, 2006; Watson & Balon, 1984) related to vertical position, locomotion and orientation of species (Appendix S3). In addition, we assigned species into trophic groups (allochthonous invertivores, autochtonous invertivores, carnivores, general invertivores, hematophagus, omnivores, and perifitivores, see Appendix S6) based on the literature (e. g. Brejão, Gerhard, & Zuanon, 2013; Carvalho & Tejerina-Garro, 2015; Zuanon et al., 2015). When information was not available for a species, we extrapolated data for the genus or family level.

All traits were combined to generate a dissimilarity matrix using Gower distance with the R function *daisy* in *cluster* package (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2016). Prior to this step, continuous variables were z-score transformed and trophic groups were assigned as asymmetrical binary variables.

Taxonomic and functional diversity

We used Rao's quadratic entropy to partition diversity into its three components, alpha, beta and gamma diversity (De Bello et al., 2010). This index has the advantage of allowing comparison between different facets of biodiversity, which is ideal to compare taxonomic and functional diversity.

Alpha diversity, or within-community diversity, is defined as:

$$\alpha Rao = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij} p_{ic} p_{jc}$$

where p_{ic} and p_{jc} are the relative proportions of species i and j in community c, and d_{ij} is the distance (functional or taxonomic) between species i and j. This index represents the expected dissimilarity of two individuals chosen randomly in a community. Gamma diversity is calculated through a similar formula, but pooling local communities together.

The calculation of beta diversity is based on the additive partitioning of gamma diversity:

$$\beta Rao = \gamma Rao - \alpha Rao$$

We expressed beta diversity as a percentage of gamma diversity. To assure that beta diversity was independent of alpha diversity, we applied the correction with equivalent numbers proposed by Jost (2007). All calculations were done using the R function *rao* (De Bello et al., 2010).

Data analyses

Regarding environmental factors, all proportion variables were transformed using log (ln (x+1)) or square-root (proportion of coarse fragments) transformation to improve data fitness to normal distribution. After that, all variables were transformed into z-scores. We reduced the number of local physical habitat variables with three steps (Appendices S4 and S5), leaving 10 variables for posterior analyses (Table 1). Catchment variables with low coefficient of variation (<10%) were removed prior to analyses, leaving five variables (Table 1).

We applied a forward selection procedure (Blanchet, Legendre, & Borcard, 2008) to retain the most important explanatory variables for the four indices of diversity. When a subset of explanatory variables (spatial, catchment or local variables) was not significant, we concluded that the subset is not important for structuring fish assemblages. To determine relationships between the selected explanatory variables from each subset and indices of diversity, we used distance-based Analysis of Redundancy (Legendre & Legendre, 2012).

To determine the influence of spatial and environmental variables for each index of diversity, we used partial distance-based Redundancy Analysis (Borcard, Legendre, & Drapeau, 1992), partitioning the variation of biological data into eight fractions: a) local physical habitat variables; b) catchment variables; c) spatial variables; d) local + catchment; e) catchment + spatial; f) local + spatial; g) local + catchment + spatial; and h) residuals. To test the significance of individual fractions (i.e. a, b and c), we used Analysis of Variance with 999 permutations (Zar, 2009). To run this analysis, we used functions *varpart*, *capscale* and *anova* of *vegan* package (Oksanen et al., 2016). All analyses were run in software R (R Development Core Team, 2016), with α = 0.05.

Table 1. Selected local physical habitat and catchment variables, with mean ± standard deviation for each river basin. LWF = large woody fragments.

Variable name	Code	Acará	Anapu	Capim	Juruena	Negro	Tapajós
Mean wetted area of longitudinal section (m²)	XWXD	1.33 ± 0.9	2.46 ± 1.16	0.64 ± 0.43	0.56 ± 0.43	0.71 ± 0.5	0.96 ± 0.51
Channel slope (%)	Slope_l	2.53 ± 2.06	1.15 ± 0.43	6 ± 2.89	5.76 ± 4.95	15.49 ± 10	11.41 ± 6.75
Substrate > 16mm diameter (bedrock, boulder, cobble, and coarse gravel) (%)	Boulders	0.53 ± 1.29	0 ± 0	3.52 ± 5.7	4.35 ± 8.76	0 ± 0	2.89 ± 2.78
Sand (%)	Sand	27.4 ± 16.01	0 ± 0	22.16 ± 19.2	24.1 ± 15.31	38.09 ± 11.69	36.99 ± 19.09
Fine litter (%)	Litter	30 ± 14.9	17.05 ± 15.83	11.41 ± 11.46	9.22 ± 5.39	8.42 ± 4.75	10.78 ± 8.92
Fast channel habitats (falls, cascades, rapids, and riffles) (%)	Fast	31.69 ± 28.15	7.53 ± 22.45	23.8 ± 17.62	50.86 ± 27.02	54.67 ± 18.1	46.95 ± 29.44
Pool (%)	Pool	5.13 ± 8.96	0.47 ± 0.63	6.8 ± 5.8	2.67 ± 2.61	0.33 ± 0.57	11.33 ± 7.24
Water velocity (m/s)	Vel	0.12 ± 0.07	0.09 ± 0.05	0.08 ± 0.06	0.22 ± 0.1	0.26 ± 0.22	0.3 ± 0.09
Mean large woody fragments (> 0.3 m diameter)	Wood	24.07 ± 21.59	44.8 ± 31.11	13.14 ± 14.68	2.11 ± 3.05	4.11 ± 2.03	3.34 ± 4.9
Altitude (m)	Altitude	39.6 ± 8.71	25.1 ± 5.55	119.6 ± 13.47	279.71 ± 70.85	72 ± 12.81	58.71 ± 29.94
Catchment slope (%)	Slope_c	5.38 ± 0.98	6.85 ± 0.59	5.96 ± 1.05	10.21 ± 2.58	11.1 ± 1.1	10.68 ± 3.16
Drainage area (Km²)	Drain_area	2.12 ± 2.26	9.62 ± 10.64	1.57 ± 2.76	1.57 ± 0.81	1.13 ± 1.51	13.02 ± 17.75
Coarse fragments in soil (> 2 mm, %)	Coarse	0.13 ± 0.38	0.9 ± 0.34	0.1 ± 0.19	0.18 ± 0.25	0.02 ± 0.04	0.56 ± 0.24
Silt in soil (%)	Silt	21.23 ± 1.39	22.32 ± 1.36	19.71 ± 0.6	24.56 ± 1.6	20.09 ± 1.54	14.93 ± 1.78

Results

We sampled 15,645 individuals, distributed in seven orders, 26 families and 111 species (Appendix S6). Acará basin showed the highest richness (49 species), and Juruena the lowest (20 species). The species *Apistograma* gr. *regani*, *Copella arnoldi*, and *Hyphessobrycon heterorhabdus* were the most abundant. Only two species, *Erythrinus erythrinus* (Characiformes) and *Synbranchus marmoratus* (Synbranchiformes), ocurred in all six river basins. Three species, *Paracanthopoma parva*, *Pygidianops amphioxus*, and *Synbranchus marmoratus*, were not measured because the former two were too small, and the latter is the only species without fins, which could bias our analyses. These three species were excluded from all analyses.

Alpha diversity

The forward selection procedure detected a significant influence of two local (in decreasing order of importance: boulders, and slope; F = 4.00, p = 0.04, Adj $R^2 = 0.20$) and one spatial variable (MEM2; F = 6.13, p = 0.01, Adj $R^2 = 0.09$) in the taxonomic data. Catchment variables did not have association with taxonomic alpha diversity, thus this component was excluded from the subsequent analyses. Boulders and channel slope showed a strong positive association with the RDA axis (Figure 2a, Table 2). MEM2, an eigenvector related to large spatial patterns, had positive association with the first axis (Figure 2c, Table 2).

Analysis of functional data revealed a statistically significant effect of one local (boulders; F = 11.31, $p < 0.01$, Adj $R^2 = 0.18$) and two spatial variables (MEM2 and MEM46; F = 4.58, p = 0.04, Adj $R^2 = 0.12$). Catchment variables did not have a significant association with functional alpha diversity, thus this component was excluded from subsequent analyses. Percentage of boulders was positively associated with the RDA ordination (Figure 2b, Table 2). MEM2 was positively associated with the RDA axis, whereas MEM46 was negatively associated with it (Figure 2d, Table 2).

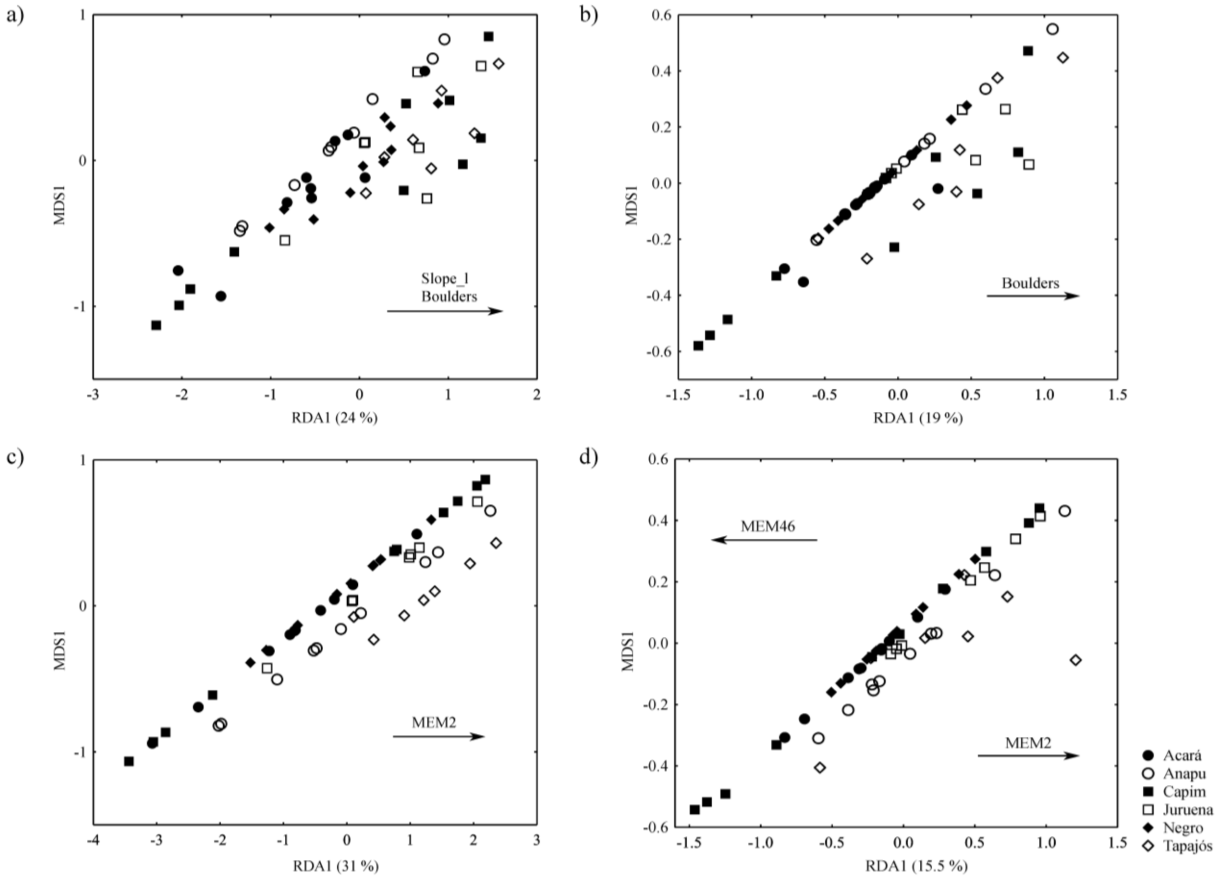

Figure 2. Redundancy Analysis for taxonomic (a, c) and functional (b, d) alpha diversity. Results are shown only for local physical habitat (a, b) and spatial variables (c, d); catchment variables were not significantly related with alpha diversity. Codes for local variables are listed in Table 1.

Table 2. Loadings of Redundancy Analysis with local physical habitat and spatial variables for alpha diversity of stream fish sampled in Eastern Amazon.

	Taxonomic data		Functional data
	RDA1		RDA1
Slope_l	0.32	Boulders	0.42
Boulders	0.42		
MEM2	0.32	MEM2	0.28
		MEM46	-0.28

Taxonomic alpha diversity was influenced mainly by local physical habitat variables (Adj $R^2 = 0.18$), followed by space (Adj $R^2 = 0.06$), with little contribution from the joint component [local + spatial] (Figure 3). For functional alpha diversity, local and spatial variables showed similar correlations with functional traits, with greater influence from environment (Adj $R^2 = 0.16$) than from space (Adj $R^2 = 0.12$). Joint influence of local and spatial variables had no influence for functional alpha diversity (Figure 3).

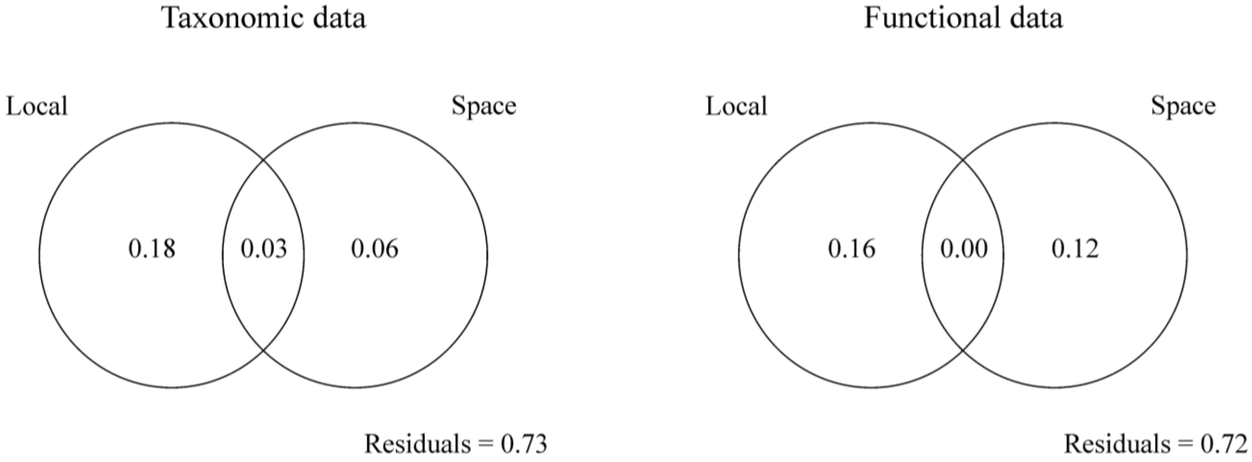

Figure 3. Partial Redundancy Analysis for taxonomic and functional alpha diversity of stream fish constrained by local physical habitat and space.

Beta diversity

Forward selection procedure retained five local variables (slope_l, water velocity, pool, fast, wood; F = 3.13, $p = 0.01$, Adj $R^2 = 0.36$), all five catchment variables (slope_c, altitude, silt, coarse, drain_area; F = 2.17, $p = 0.04$, Adj $R^2 = 0.47$), and three spatial variables (MEM1, MEM2, MEM3; F = 9.50, $p < 0.01$, Adj $R^2 = 0.50$) with significant associations with taxonomic beta diversity. All three ordinations with taxonomic beta diversity showed similar patterns. For local variables, the first axis formed a gradient related to shear stress, with steeper slopes and faster water velocity (Table 3) on the right side, associated with streams from Juruena, Negro and Tapajós river basins. Streams from Anapu, Acará and Capim river basins had slower water velocity and a larger proportion of large wood (Figure 4a). The second axis was formed by proportion of pools (positive association; Table 3), closely associated to Acará, Capim, and Tapajós river basins. When considering the catchment variables, the first axis separated Tapajós, Juruena and Negro streams, with steep catchment slopes (Table 3), from Acará, Capim and Anapu river basins (Figure 4c). In the second axis, Anapu and Acará showed the highest drainage areas and proportion of coarse fragments in soil, whereas Capim and Juruena had the highest altitudes (Table 3). Spatial variables again separated Juruena, Tapajós, and Anapu river basins from the remaining basins (Figure 4e, Table 3).

For functional beta diversity, three local (wood, boulders, water velocity; $F = 3.50$, $p < 0.01$, Adj $R^2 = 0.20$), three catchment (altitude, slope_c, coarse; $F = 3.61$, $p = 0.01$, Adj $R^2 = 0.29$), and three spatial variables (MEM3, MEM2, MEM1; $F = 8.32$, $p < 0.01$, Adj $R^2 = 0.35$) were selected. The distribution of sites in ordination space resembled the pattern obtained for taxonomic beta diversity, but the patterns were less distinct. For local physical habitat (Figure 4b), the first axis showed contrasting patterns for substrates, with boulders associated with Juruena, Capim, and Tapajós river basins, whereas Acará and Anapu had a higher proportion of large wood. Juruena, Negro, and Tapajós river basins had more fast habitat channels (Table 3) than the other basins. The second ordination (Figure 4d) separated the higher altitude streams from Juruena and Capim (Table 3), from the other basins, whereas Juruena, Negro, and Tapajós streams had steeper catchment slopes. Anapu and Negro had greater proportions of coarse fragments in soil. The third ordination (Figure 4f) also separated Juruena, Negro, and Tapajós river basins from streams of other basins regarding MEM1, MEM2, and MEM3.

Table 3. Redundancy Analysis loadings of local physical habitat, catchment and spatial variables for beta diversity of stream fish. Codes for local and catchment variables are listed in Table 1.

	Taxonomic data			Functional data		
	Variable	RDA1	RDA2	Variable	RDA1	RDA2
Local	Slope_l	0.69	0.14	Boulders	0.34	-0.37
	Fast	0.59	0.33	Vel	0.45	0.33
	Pool	-0.10	0.52	Wood	-0.63	0.03
	Vel	0.58	-0.07			
	Wood	-0.64	-0.31			
Catchment	Altitude	0.41	0.74	Altitude	0.73	0.30
	Slope_c	0.85	-0.18	Slope_c	0.49	-0.55
	Drain_Area	-0.15	-0.35	Coarse	-0.21	-0.30
	Coarse	-0.14	-0.43			
	Silt	-0.05	0.03			
Spatial	MEM1	0.94	-0.07	MEM1	0.51	0.23
	MEM2	0.08	0.22	MEM2	0.09	0.65
	MEM3	0.05	0.94	MEM3	0.63	-0.28

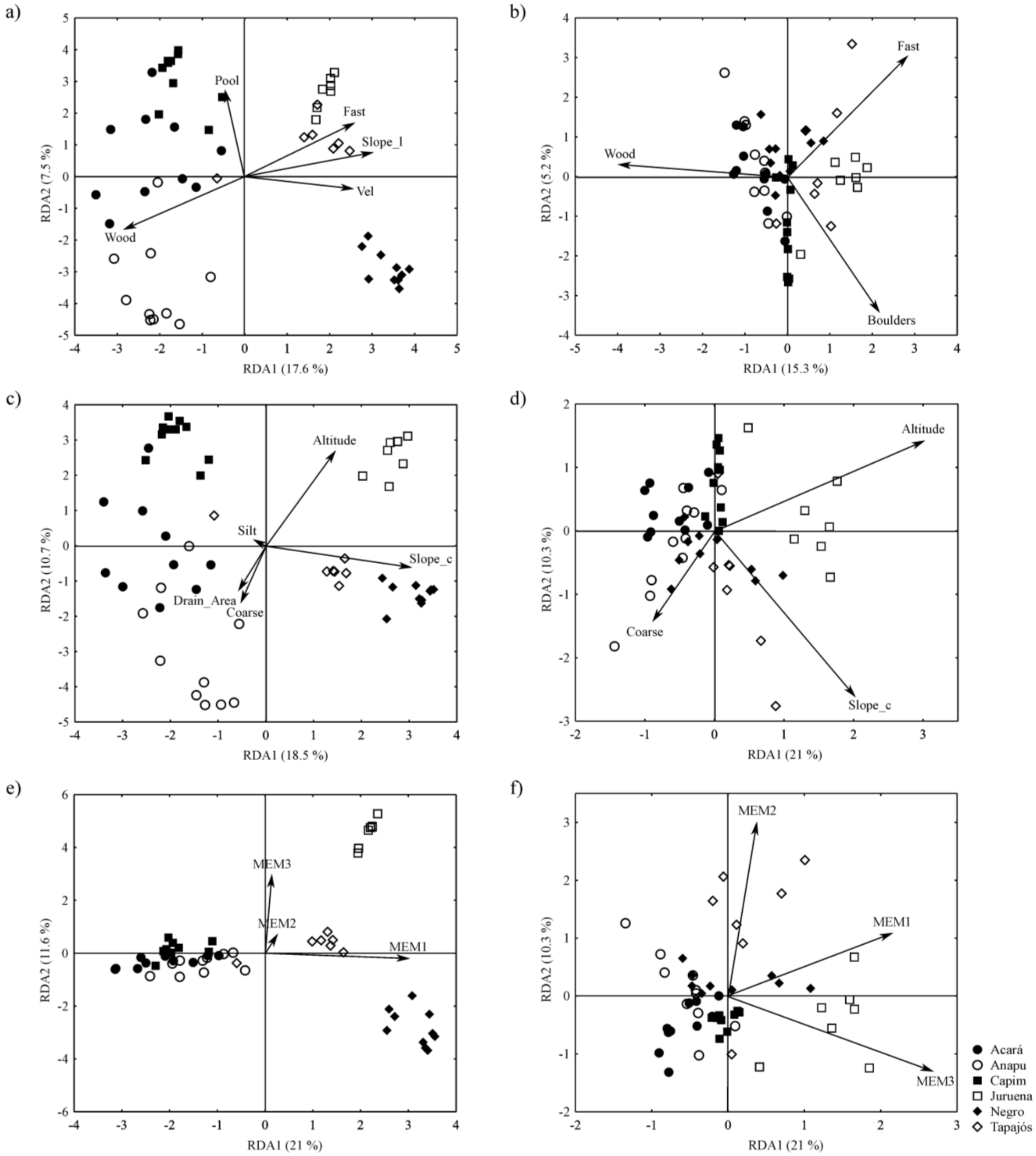

Figure 4. Ordinations of Redundancy Analysis for taxonomic (a, c, e) and functional (b, d, f) beta diversity of stream fish constrained by local physical habitat (a, b), catchment (c, d), and spatial variables (e, f). Codes for local and catchment variables are listed in Table 1.

Partial Redundancy Analysis (Figure 5) showed that the sum of environmental components [local + catchment + joint local and catchment] was the main factor affecting both taxonomic (Adj $R^2 = 0.17$) and functional (Adj $R^2 = 0.16$) beta diversity, but when the environment component was partitioned between spatial scales, space was the most important factor, both for taxonomic (Adj $R^2 = 0.12$) and functional (Adj $R^2 = 0.10$) beta diversity. Catchment had a stronger influence than local variables in both cases. The shared explanations of [catchment+space] and [local+catchment+space] were important for both components of beta diversity.

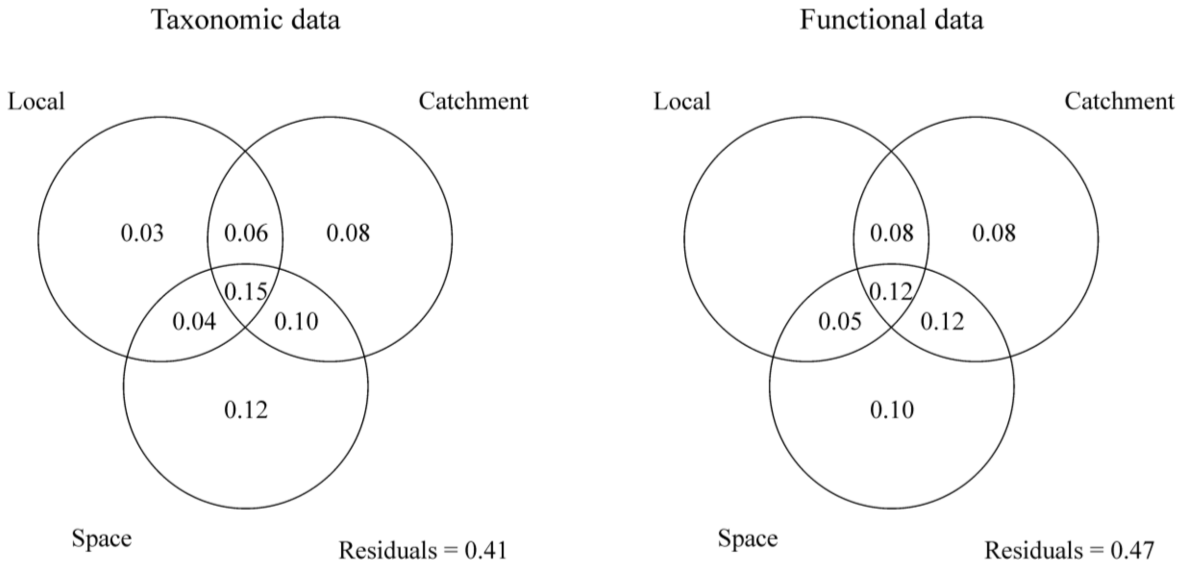

Figure 5. Partial Redundancy Analysis for taxonomic and functional beta diversity of stream fish constrained by local physical habitat, catchment and spatial variables. Negative values are not displayed.

Discussion

Our study aimed to explore the importance of environmental variables at two different scales (local and catchment) and spatial variables for taxonomic and functional alpha diversity and taxonomic and functional beta diversity of stream fishes. We detected the following patterns: 1) taxonomic and functional alpha diversity are closely associated with variation in substrate composition and spatial variables, whereas catchment variables played no influence. 2) Space is the main factor structuring taxonomic and functional beta diversity, followed by catchment variables. 3) Patterns of beta diversity are dissimilar considering environmental variables at distinct scales, indicating a lack of congruency between the various spatial scales of analysis.

Taxonomic alpha diversity decreased with boulders and channel slope, and boulders were also important to functional alpha diversity (Table 2). Steeper slopes have faster water velocity and enhanced shear stress, diminishing the presence of organic substrates (Benone et al., 2017; Hoover, Richardson, & Yonemitsu, 2006) and increasing the presence of boulders (Pease et al., 2015). Organic substrates increase habitat heterogeneity, providing opportunities for feeding and sheltering, allowing the coexistence of different species (Brejão et al., 2013; Heino & Tolonen, 2017; Leitão et al., 2017). The reduction of organic substrates and the increasing presence of boulders demands certain adaptations to life in fast waters (Pease et al., 2015), and this filtering may be responsible for lower functional and taxonomic alpha diversity. Also, streams that are more isolated have lower taxonomic and functional alpha diversity, possibly due to low connectivity and limited dispersal ability (Blanchet et al., 2014; Jaramillo-Villa, Maldonado-Ocampo, & Escobar, 2010) of stream fish.

Our analysis explained ca. 60% and 50% of the variation in taxonomic and functional beta diversity, respectively. This is greater than what other studies found for stream fish (Göthe et al., 2017; Hoeinghaus et al., 2007; Terra et al., 2016; Wang et al., 2003) and is possibly due to the inclusion of spatial variables (Sály et al., 2011). The strong influence of space on taxonomic assemblage composition likely is associated with a strong influence of species distributions within the six basins. Biogeographic patterns are affected by the dendritic nature of river networks that constrains fish dispersion (Blanchet et al., 2014; Clarke et al., 2010; Reyjol et al., 2007). Furthermore, stream fishes are typically small with limited home ranges, characteristics that limit dispersal and promote endemism (Griffiths, 2010). Therefore, species composition depends on the limits of river basins, with high dissimilarity across basins, possibly due to allopatric speciation. The importance of space in structuring local assemblages has been observed in studies of other organisms, and this importance tends to increase at larger spatial scales that encompass stronger environmental gradients and dispersal limitation (Da Silva, Almeida-Neto, & Arena, 2014; Mykrä, Heino, & Muotka, 2007; Shurin, Cottenie, & Hillebrand, 2009).

Among the environment variables tested, altitude and elevational gradient (slope) were the main drivers of variation in taxonomic and functional beta diversity. These variables are important regulators of the local physical habitat from small streams, affecting channel morphology, longitudinal gradient and substrate deposition (Frissell et al., 1986; Grabowski et al., 2014). Thus, catchment variables filter fish assemblages indirectly through their influence on conditions of local habitats. The combined effect of spatial and environmental variables on beta diversity reflects a major environmental gradient, where basins close to mountain ranges have conditions distinct from those in the lowlands. Streams with steep gradients have fast waters and less organic substrates due to increased shear stress, whereas streams with flat gradient have slower water velocities and accumulate more organic material, a pattern previously documented for the studied river basins (Benone et al., 2017). These contrasting conditions can explain why functional beta diversity was influenced more strongly than alpha diversity by the joint effect of catchment and space; environmental filtering should have greatest influence upon functional traits of isolated assemblages (Carvalho & Tejerina-Garro, 2015). Studies using aquatic and terrestrial taxa also found higher beta diversity among isolated assemblages, whereby allopatry gives rise to evolution of local adaptations (Blanchet et al., 2014; Da Silva et al., 2014; Griffiths, 2010; Weinstein et al., 2014).

Contrary to other studies (Carvalho & Tejerina-Garro, 2015; Pease, González-Díaz, Rodiles-Hernández, & Winemiller, 2012), local variables alone had little effect on beta diversity. On the other hand, the combined effect of local variables with other drivers (catchment and spatial variables) were important for fish beta diversity. Substrate and water velocity were strongly associated with fish assemblage composition, and these environmental factors have well-known roles as habitat filters of aquatic biota (Allan, 2004). In slow-flowing habitats (i.e. streams at low altitude with shallow slopes), the accumulation of organic substrates is important for fish trophic ecology, as they provide shelter for aquatic macroinvertebrates (Brejão et al., 2013; Mendes, Kiffer, & Moretti, 2017). In contrast, high altitudinal, steep streams with fast-flowing water had lower amounts of organic substrates and higher proportion of boulders, indicating the increased shear stress. These conditions require a distinct set of morphological features proper to life in fast waters (Pease et al., 2012), emphasizing the role of environmental filtering for stream fishes.

The stronger effect of catchment variables for both taxonomic and functional beta diversity compared to the influence of local variables is contrary to findings from other studies (Terra et al., 2016; Zbinden & Matthews, 2017). Studies that show high influence of local variables usually consider small spatial extents (Pease et al., 2012; Sály et al., 2011; Terra et al., 2016). When larger spatial extents are encompassed, as in the present study, associations of environmental variables with beta diversity tends to be stronger (Ferreira et al., 2007; Oliveira et al., 2012; but see Carvalho & Tejerina-Garro, 2015). This difference may be because environmental factors that vary at large scales have relatively low variability at smaller scales, and environmental heterogeneity generally is perceived at local scales. The strong environmental variation occurring at the catchment scale may also reflect conditions that vary over longer time scales, and in the short-term may seem relatively stable compared to snapshots of local conditions (Jyrkänkallio-Mikkola et al., 2017).

In summary, we found that dispersal limitation and environmental filtering are complementary for stream fish taxonomic and functional diversity, revealing the importance of including both environmental and spatial variables. Taxonomic and functional alpha diversity are strongly associated with variation in local physical habitat, whereas taxonomic and functional beta diversity tend to be more strongly associated with variation among environmental variation at the catchment scale. More importantly, space was influential in all cases, highlighting the potential role of dispersal as a constraint on assemblage structure of stream fish. We encourage future studies to account for the responses of multiple facets of biodiversity to different drivers (e.g. Blanchet et al., 2014; Cilleros et al., 2016; Sály et al., 2011) in order to provide the most useful informations for biodiversity conservation.

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SUPPORTING INFORMATION

Assessment of local physical habitat variables

We measured 35 physical habitat variables divided in six blocks: channel morphology (e.g. width, depth), substrate (e.g. bedrock, sand), channel habitat units (e.g. riffle, pool), riparian vegetation cover (e.g canopy cover), large woody fragments (> 1.5 m long and > 10 cm at the small-end diameter), and instream cover for aquatic organisms (e.g. coarse and fine litter) (Appendix S1). Wetted width and substrate were measured 21 times, 11 in the regular cross-sections and 10 in supplementary cross-sections in the middle of each 15m-longitudinal section. Wetted width was measured with a surveyor's tape. Substrate was assessed by placing a calibrated pole in five equidistant points along the cross-sections and it was classified in several groups: smooth and rough bedrock, boulder, cobble, coarse and fine gravel, sand, silt/muck/clay, roots, coarse and fine litter, roots, and algae. Instream cover was visually determined in an area of 5 m up- and downstream of each regular cross-section, being classified as small (< 30 cm at small-end diameter) and large (> 30 cm at small-end diameter) woody fragments, living trees and roots, coarse litter, overhanging vegetation (up to 1m above channel), undercut banks, and boulder. Depth was measured at five equidistant points along the regular 11 cross-sections transects and at 15 equidistant points along the thalweg in the longitudinal sections. In these 15 points, we visually classified the flow in the following habitat channel units: falls, cascades, rapids, riffles, glides, pools. Mean wetted area of longitudinal section was calculated as the mean product between all measures of width and depth. Along the longitudinal sections, we counted the number of large woody fragments (> 0.3 m at small-end diameter and > 1.5 m length) and calculated the volume of wood following Kaufmann, Levine, Peck, Robison, and Seeliger (1999). Slope was determined at each longitudinal section with a water hose and two rulers. Discharge, the product of the mean current velocity and vertical cross-sectional area, was obtained with the neutrally-flowing buoyant procedure (Peck et al., 2006).

Appendix S1. Local physical habitat variables used to characterize 54 streams in six river basins in Amazon. Values represent mean ± standard deviation.

Block of variables	Variable name	Variable code	Acará	Anapu	Capim	Juruena	Negro	Tapajós
Channel morphology	Mean depth of thalweg (cm)	XDEPTH_TH	33.21 ± 14.21	54.36 ± 15.96	25.58 ± 11.09	21.76 ± 8.12	31.41 ± 13.63	10.71 ± 2.94
	Mean wetted width (m)	XWIDTH	3.44 ± 1.06	4.52 ± 2.06	2.25 ± 0.54	2.29 ± 1.08	2.01 ± 0.59	0.96 ± 0.51
	Mean wetted area of longitudinal section (m^2)	XWXD	1.33 ± 0.9	2.46 ± 1.16	0.64 ± 0.43	0.56 ± 0.43	0.71 ± 0.5	0.96 ± 0.51
	Mean longitudinal section width x depth ratio (m/m)	XWD_RAT	12.43 ± 6.01	8.96 ± 4.66	9.49 ± 1.89	10.55 ± 2.72	7.15 ± 1.45	7.65 ± 2.24
	Channel slope (%)	XSLOPE	2.53 ± 2.06	1.15 ± 0.43	6 ± 2.89	5.76 ± 4.95	15.49 ± 10	11.41 ± 6.75
Substrate	Mean embeddedness (channel and banks) (%)	XEMBED	50.76 ± 25.31	62.25 ± 21.86	53.3 ± 14.63	67.98 ± 16.06	61.07 ± 11.76	66.13 ± 10.89
	Substrate > 16mm diameter (bedrock, boulder, cobble, and coarse gravel) (%)	PCT_BIGR	0.53 ± 1.29	0 ± 0	3.52 ± 5.7	4.35 ± 8.76	0 ± 0	2.89 ± 2.78
	Sand (%)	PCT_SA	27.4 ± 16.01	0 ± 0	22.16 ± 19.2	24.1 ± 15.31	38.09 ± 11.69	36.99 ± 19.09
	Silt/muck/clay (%)	PCT_ST	6.2 ± 4.1	26.1 ± 31.18	9.59 ± 6.97	25.29 ± 4.17	0.67 ± 1.01	10.8 ± 17
	Substrate < 16 mm diameter (fine gravel, sand, and silt/muck/clay) (%)	PCT_SFGF	33.73 ± 16.85	26.1 ± 31.18	37.76 ± 12.06	51.6 ± 16.15	38.75 ± 11.62	49.3 ± 11.37
	Total organic matter (litter, wood, roots, and algae) (%)	PCT_ORG	64.67 ± 17.74	72.95 ± 30.51	51.34 ± 10.16	44.05 ± 18.44	61.06 ± 11.59	47.81 ± 12.71
	Roots (%)	PCT_RO	6.13 ± 5.45	6.86 ± 9.64	6.48 ± 4.7	3.13 ± 4.72	36.57 ± 9.76	22.36 ± 7.59
	Fine litter (%)	PCT_FL	30 ± 14.9	17.05 ± 15.83	11.41 ± 11.46	9.22 ± 5.39	8.42 ± 4.75	10.78 ± 8.92
	Coarse litter (%)	PCT_CL	17.33 ± 7.28	27.9 ± 23.33	28.26 ± 10.77	26.49 ± 15.98	10.8 ± 4.32	8.8 ± 6.58

Appendix S1. Continuation.

Block of variables	Variable name	Variable code	Acará	Anapu	Capim	Juruena	Negro	Tapajós
Channel habitat units and water velocity	Glides (%)	PCT_GL	63.18 ± 25	92 ± 22.76	69.4 ± 14.9	46.48 ± 27.01	45 ± 18.08	41.71 ± 26.17
	Fast channel habitats (falls, cascades, rapids, and riffles) (%)	PCT_FAST	31.69 ± 28.15	7.53 ± 22.45	23.8 ± 17.62	50.86 ± 27.02	54.67 ± 18.1	46.95 ± 29.44
	All pool types (%)	PCT_POOL	5.13 ± 8.96	0.47 ± 0.63	6.8 ± 5.8	2.67 ± 2.61	0.33 ± 0.57	11.33 ± 7.24
	Sequence fast flow, slow flow, and pools (1= maximum heterogeneity, 0= maximum homogeneity)	SEQ_FLO_1	0.13 ± 0.07	0.02 ± 0.04	0.16 ± 0.06	0.17 ± 0.09	0.16 ± 0.08	0.08 ± 0.05
	Discharge (m^3/s)	DIS	0.08 ± 0.06	0.12 ± 0.11	0.04 ± 0.04	0.04 ± 0.02	0.05 ± 0.08	0.14 ± 0.1
	Water velocity (m/s)	VEL	0.12 ± 0.07	0.09 ± 0.05	0.08 ± 0.06	0.22 ± 0.1	0.26 ± 0.22	0.3 ± 0.09
Riparian vegetation cover	Mean canopy cover (%)	XC	71.14 ± 34.45	73.76 ± 11.55	67.77 ± 13.59	89.25 ± 18.08	82.99 ± 12.33	94.59 ± 17.72
	Mean understory cover (%)	XM	60.89 ± 24.68	93.05 ± 18.66	71.99 ± 14.39	93.18 ± 12.48	96.31 ± 16.29	83.08 ± 12.21
	Mean ground cover (%)	XG	41.89 ± 29.2	70.78 ± 24.9	40.59 ± 6.33	63.7 ± 10.71	85.86 ± 21.18	53.17 ± 7.53
	Mean total riparian cover (%)	XCMG	173.91 ± 75.33	237.59 ± 34.21	180.35 ± 23.07	246.14 ± 29.91	265.16 ± 41.55	230.84 ± 24.86
Large woody pieces	Number LWP inside bankfull channel / 150m - size class 1	C1W_150	45.07 ± 29.7	33.47 ± 21.11	20.73 ± 13.25	12.86 ± 6.71	21.07 ± 9	10.86 ± 3.52
	Volume LWP inside bankfull channel / 150m - size class 1	V1W_150	10.93 ± 9.9	22.3 ± 22.74	2.81 ± 2.28	6.26 ± 5.27	2.78 ± 1.53	1.32 ± 0.67
Instream cover for aquatic organisms	Mean large woody fragments (> 0.3 m diameter) (%)	XFC_LWF	24.07 ± 21.59	44.8 ± 31.11	13.14 ± 14.68	2.11 ± 3.05	4.11 ± 2.03	3.34 ± 4.9
	Mean small woody fragments (< 0.3 m diameter) (%)	XFC_SWF	35.93 ± 21.45	50.34 ± 27.6	19.11 ± 12.25	21.98 ± 12.31	22.93 ± 6.39	27.92 ± 6.63
	Mean trees and roots (%)	XFC_TR	19.93 ± 12.75	47.93 ± 22.38	10.39 ± 7.68	13.21 ± 10.29	46.86 ± 15.5	26.04 ± 9.42
	Mean coarse litter (%)	XFC_CL	36.73 ± 21.21	57.16 ± 24.94	43.45 ± 21.4	41.53 ± 23.76	19.61 ± 10.33	17.34 ± 9.57

Appendix S1. Cont.

Block of variables	Variable name	Variable code	Acará	Anapu	Capim	Juruena	Negro	Tapajós
Instream cover for aquatic organisms	Mean overhanging vegetation (up to 1m above channel) (%)	XFC_OV	22 ± 9.06	37 ± 16	16.43 ± 7.64	19.19 ± 13.44	43.36 ± 15.38	20.55 ± 13.26
	Mean undercut banks (%)	XFC_UB	2.48 ± 2.7	0 ± 0	8.86 ± 5.48	2.99 ± 1.55	1.14 ± 0.94	1.88 ± 1.65
	Mean boulder (%)	XFC_BO	1.16 ± 3.21	0 ± 0	0.41 ± 0.73	2.08 ± 5.1	0 ± 0	0 ± 0
	Mean natural cover (woody fragments, trees and roots, coarse litter, overhanging vegetation, undercut banks, and boulder) (%)	XFC_NAT	142.3 ± 58.19	249.64 ± 109.92	111.8 ± 42.23	154.64 ± 27.6	98.09 ± 42.47	97.08 ± 28.36
	Proportion of large fish cover (large woody fragments, undercut banks, boulder and artificial structures) (%)	PFC_LAR	0.85 ± 0.18	0.94 ± 0.12	0.93 ± 0.07	0.64 ± 0.2	0.52 ± 0.22	0.49 ± 0.23

Appendix S2. Catchment variables used to characterize 54 streams across six river basins in Amazon. Values represent mean ± standard deviation.

	Acará	**Anapu**	**Capim**	**Juruena**	**Negro**	**Tapajós**
Mean annual air temperature (ºC)	26.84 ± 0.05	26.76 ± 0.05	26.74 ± 0.07	25.21 ± 0.37	27.19 ± 0.09	25.84 ± 0.21
Temperature of driest quarter (ºC)	27.07 ± 0.08	27.27 ± 0.05	26.94 ± 0.07	24.76 ± 0.33	27.78 ± 0.08	26.44 ± 0.21
Mean annual precipitation (mm)	2487.1 ± 28.81	2205.8 ± 27.8	2082.9 ± 55.16	2224.43 ± 10.71	2184.7 ± 6.57	1951.86 ± 55.32
Precipitation of driest quarter (mm)	179.4 ± 16.11	200.7 ± 10.81	81.5 ± 3.75	64.14 ± 0.38	251.8 ± 6.29	149.14 ± 10.25
Altitude (m)	39.6 ± 8.71	25.1 ± 5.55	119.6 ± 13.47	279.71 ± 70.85	72 ± 12.81	58.71 ± 29.94
Catchment slope (%)	5.38 ± 0.98	6.85 ± 0.59	5.96 ± 1.05	10.21 ± 2.58	11.1 ± 1.1	10.68 ± 3.16
Drainage area (Km²)	2.12 ± 2.26	9.62 ± 10.64	1.57 ± 2.76	1.57 ± 0.81	1.13 ± 1.51	13.02 ± 17.75
Proportion of clay in soil (%)	31.65 ± 1.21	32.84 ± 1.01	33.94 ± 1.61	29.85 ± 0.98	31.94 ± 0.9	36.3 ± 4.5
Proportion of sand in soil (%)	47.1 ± 1.53	44.85 ± 2.19	46.19 ± 1.39	45.49 ± 1.77	48.13 ± 1.95	48.79 ± 5.86
Proportion of coarse fragments in soil (> 2 mm, %)	0.13 ± 0.38	0.9 ± 0.34	0.1 ± 0.19	0.18 ± 0.25	0.02 ± 0.04	0.56 ± 0.24
Proportion of silt in soil (%)	21.23 ± 1.39	22.32 ± 1.36	19.71 ± 0.6	24.56 ± 1.6	20.09 ± 1.54	14.93 ± 1.78

Appendix S3. Ecomorphological indices based on 16 morphological measures. All indices followed Watson and Balon (1984) and Ohlberger, Staaks, and Hölker (2006).

Index	Variable code	Formula	Interpretation
Compression index	CI	MBH/MBW	High values indicate compressed fish which prefer habitats with slow flows
Relative height	RH	MBH/SL	Low values are related to fish inhabiting faster waters and lower capacity of vertical turns
Relative length of caudal peduncle	RLCP	LCP/SL	High values are associated to higher swimming capacity or fishes inhabiting faster waters, but not necessarily nektonic, able to realize propulsion at short distances
Compression index of caudal peduncle	CICP	MHCP/MWCP	Higher values indicate fish with compresses peduncles, typical of fish with slow swimming and low maneuverability
Index of ventral flattening	IVF	HBM/MBH	Lower values indicate fish adapted to fast waters, which can maintain position without swimming, typical of benthic species
Relative area of pectoral fin	RAPF	PFA/BA	High values are related to slow swimming species with good maneuverability or fish adapted to fast waters that live closer to the bottom
Aspect ratio of pectoral fin	ARPF	LPF/HPF	Higher ratios are associated to continuous high-speed swimmers that prefer pelagic regions
Relative length of head	RLH	HL/SL	Fish with larger heads ingest larger preys, thus this index is more related to piscivores
Relative position of eyes	RPE	HEM/HH	High values indicate dorsal eyes, typical of benthic species
Relative width of mouth	RWM	MW/SL	Higher values are associated to fish that ingest larger preys, as piscivorous species
Mouth orientation	MO	°	High values are related to fish that feed closer to the surface. Code: ventral = 0º; inferior = 10 – 80º; terminal = 90º; superior = 100 – 170º
Fineness coefficient	FC	SL/√MBH*MBW	This index evaluates the influence of body shape to swimming efficiency. Values of 2 to 6 indicate reduced drag, optimum ratio is 4.5

Selection of local physical habitat variables

All proportion values for variables were transformed (ln (x+1)) to improve data fitness to normal distribution. Other values for other variables were transformed into z-scores. To reduce the number of variables, we excluded those with high collinearity (Spearman's $r \geq 0.7$), excluding eight variables (Appendix S4). After that, we selected the environmental variables with a significant contribution to ichthyofauna. Taxonomic data was transformed (log (x+1)) prior to analysis to reduce the skewness of their distribution. For functional traits, we used community weighted mean (CWM, Lavorel et al., 2008) to obtain a matrix of sites versus traits, as explained in the main text (see "Functional traits"). We used Forward selection (Blanchet, Legendre, & Borcard, 2008) per block to select the most important environmental variables. Since the blocks "Riparian vegetation cover" and "Large woody fragments" only had two variables each, we concatenated them with "Instream cover", since the three blocks are related to the contribution of riparian cover. We retained variables with significant correlations ($\alpha = 0.05$) with the two biological data, selecting nine variables (Appendix S5). Analyses were run using function *forward.sel* in package *packfor* (Dray, Legendre, & Blanchet, 2016).

Appendix S4. Correlations between pairs of local physical habitat variables. Bold values indicate strong correlations (r ≥ 0.7). Codes for variables are listed in Appendix S1.

	XDEPTH_TH	XWIDTH	XWXD	XWD_RAT	XEMBED	PCT_BIGR	PCT_SA	PCT_ST	PCT_SFGF	PCT_ORG
XWIDTH	**0.80**									
XWXD	**0.77**	**0.73**								
XWD_RAT	-0.26	0.21	-0.19							
XEMBED	0.02	-0.11	0.03	-0.28						
PCT_BIGR	-0.50	-0.36	-0.24	0.22	-0.18					
PCT_SA	-0.28	-0.37	-0.18	-0.12	0.15	0.09				
PCT_ST	-0.07	0.08	-0.04	0.07	0.36	0.18	-0.30			
PCT_SFGF	-0.27	-0.32	-0.16	-0.16	0.51	0.29	0.60	0.39		
PCT_ORG	0.36	0.34	0.24	0.03	-0.40	-0.54	-0.48	-0.44	**-0.91**	
PCT_RO	-0.11	-0.42	-0.10	-0.53	-0.14	-0.05	0.40	-0.51	-0.03	0.12
PCT_FL	0.04	0.19	0.05	0.26	-0.20	-0.05	-0.35	-0.10	-0.50	0.51
PCT_CL	0.12	0.24	-0.06	0.31	-0.34	-0.16	-0.35	0.00	-0.50	0.41
PCT_GL	0.31	0.43	0.25	0.14	-0.05	-0.13	-0.63	0.21	-0.30	0.25
PCT_FAST	-0.22	-0.38	-0.22	-0.16	0.12	0.06	0.62	-0.23	0.30	-0.24
PCT_POOL	-0.55	-0.40	-0.35	0.15	-0.10	0.36	0.06	0.11	0.03	-0.14
SEQ_FLO_1	-0.33	-0.43	-0.59	0.10	-0.20	0.16	0.25	-0.08	-0.03	-0.02
DIS	0.35	0.26	0.62	-0.33	0.25	0.03	-0.05	0.12	0.08	-0.05
VEL	-0.17	-0.32	0.04	-0.28	0.41	-0.02	0.47	-0.06	0.38	-0.23
XSLOPE	-0.63	**-0.78**	-0.62	-0.11	-0.10	0.23	0.53	-0.30	0.19	-0.24
XC	-0.15	-0.14	0.02	-0.22	-0.12	-0.03	0.23	0.01	0.17	-0.10
XM	0.07	-0.15	-0.04	-0.34	0.09	-0.02	-0.06	-0.06	0.01	0.04
XG	0.14	-0.16	0.01	-0.40	0.02	-0.19	0.11	-0.18	0.01	0.15
XCMG	0.10	-0.14	0.06	-0.44	0.06	-0.13	0.13	-0.12	0.06	0.07
C1W_150	0.59	0.56	0.39	0.02	-0.24	-0.25	-0.21	-0.19	-0.38	0.38
V1W_150	0.57	0.66	0.41	0.02	0.01	-0.29	-0.43	0.27	-0.18	0.26
XFC_LWF	0.52	0.57	0.41	0.01	-0.10	-0.25	-0.31	0.06	-0.21	0.22
XFC_SWF	0.30	0.27	0.39	-0.18	-0.16	-0.19	-0.17	0.05	-0.10	0.19
XFC_TR	0.41	0.15	0.39	-0.44	-0.10	-0.37	-0.11	-0.29	-0.26	0.40
XFC_CL	0.19	0.31	0.04	0.23	-0.26	-0.17	-0.57	0.27	-0.46	0.40
XFC_OV	0.44	0.20	0.32	-0.31	0.09	-0.42	-0.03	-0.14	-0.14	0.28
XFC_UB	-0.30	-0.29	-0.40	0.02	-0.26	0.29	0.27	0.12	0.16	-0.28
XFC_BO	-0.21	-0.10	-0.31	0.31	-0.19	0.56	-0.01	0.16	0.11	-0.26
XFC_NAT	0.32	0.41	0.30	0.12	-0.08	-0.16	-0.39	0.38	-0.10	0.14
PFC_LAR	0.47	0.58	0.35	0.02	-0.01	-0.12	-0.41	0.27	-0.17	0.10

Appendix S4. Continuation

	PCT_FL	PCT_CL	PCT_GL	PCT_FAST	PCT_POOL	SEQ_FLO_1	DIS	VEL	XSLOPE	XC
XWIDTH										
XWXD										
XWD_RAT										
XEMBED										
PCT_BIGR										
PCT_SA										
PCT_ST										
PCT_SFGF										
PCT_ORG										
PCT_RO										
PCT_FL										
PCT_CL	0.00									
PCT_GL	0.05	0.42								
PCT_FAST	-0.06	-0.44	**-0.97**							
PCT_POOL	-0.01	0.14	-0.08	-0.11						
SEQ_FLO_1	0.08	0.06	-0.34	0.31	0.33					
DIS	0.09	-0.29	-0.12	0.11	-0.15	-0.35				
VEL	-0.11	-0.45	-0.55	0.57	-0.08	0.03	0.50			
XSLOPE	-0.31	-0.22	-0.60	0.56	0.33	0.50	-0.40	0.24		
XC	-0.33	-0.04	-0.18	0.10	0.09	-0.12	0.01	0.25	0.22	
XM	-0.03	-0.12	-0.02	0.04	-0.15	-0.02	-0.01	0.16	0.07	0.33
XG	-0.15	-0.15	-0.19	0.19	-0.21	0.02	0.00	0.25	0.16	0.28
XCMG	-0.14	-0.14	-0.12	0.10	-0.13	-0.05	0.04	0.27	0.10	0.62
C1W_150	0.18	0.23	0.24	-0.22	-0.25	-0.07	0.12	-0.35	-0.38	-0.34
V1W_150	0.28	0.14	0.31	-0.27	-0.29	-0.30	0.14	-0.36	-0.62	-0.17
XFC_LWF	0.19	0.13	0.41	-0.40	-0.20	-0.34	0.19	-0.38	-0.56	-0.18
XFC_SWF	0.11	-0.08	0.09	-0.11	-0.25	-0.44	0.34	-0.03	-0.30	0.36
XFC_TR	-0.07	-0.23	-0.02	0.07	-0.39	-0.23	0.19	0.11	0.04	0.26
XFC_CL	0.18	0.66	0.53	-0.56	0.17	-0.07	-0.22	-0.55	-0.33	0.02
XFC_OV	-0.01	-0.24	0.00	0.07	-0.32	-0.14	0.10	0.10	-0.02	0.23
XFC_UB	-0.02	0.15	-0.19	0.14	0.28	0.52	-0.20	-0.07	0.22	0.02
XFC_BO	0.04	0.17	0.04	-0.07	0.23	0.28	-0.29	-0.24	0.03	-0.17
XFC_NAT	0.05	0.18	0.22	-0.22	-0.12	-0.29	0.08	-0.20	-0.39	0.15
PFC_LAR	0.12	0.26	0.36	-0.36	-0.02	-0.31	0.20	-0.51	-0.57	-0.26

Appendix S4. Cont.

	XM	XG	XCMG	C1W_150	V1W_150	XFC_LWF	XFC_SWF	XFC_TR	XFC_CL	XFC_OV
XWIDTH										
XWXD										
XWD_RAT										
XEMBED										
PCT_BIGR										
PCT_SA										
PCT_ST										
PCT_SFGF										
PCT_ORG										
PCT_RO										
PCT_FL										
PCT_CL										
PCT_GL										
PCT_FAST										
PCT_POOL										
SEQ_FLO_1										
DIS										
VEL										
XSLOPE										
XC										
XM										
XG	0.66									
XCMG	**0.84**	**0.81**								
C1W_150	-0.07	0.02	-0.09							
V1W_150	-0.03	0.06	-0.02	0.50						
XFC_LWF	-0.20	-0.20	-0.17	0.35	0.51					
XFC_SWF	0.18	0.17	0.30	0.27	0.38	0.49				
XFC_TR	0.34	0.56	0.47	0.27	0.28	0.19	0.53			
XFC_CL	0.05	-0.04	0.02	0.27	0.46	0.36	0.24	0.05		
XFC_OV	0.34	0.43	0.45	0.11	0.28	0.19	0.33	**0.71**	0.14	
XFC_UB	-0.09	-0.25	-0.13	-0.08	-0.36	-0.20	-0.20	-0.52	-0.14	-0.48
XFC_BO	0.03	-0.11	-0.12	-0.07	-0.06	-0.06	-0.27	-0.44	-0.01	-0.35
XFC_NAT	0.09	0.11	0.14	0.15	0.56	0.53	0.59	0.32	0.53	0.22
PFC_LAR	-0.17	-0.35	-0.29	0.34	0.52	**0.70**	0.19	-0.10	0.38	0.05

Appendix S4. Cont.

	XFC_UB	XFC_BO	XFC_NAT
XWIDTH			
XWXD			
XWD_RAT			
XEMBED			
PCT_BIGR			
PCT_SA			
PCT_ST			
PCT_SFGF			
PCT_ORG			
PCT_RO			
PCT_FL			
PCT_CL			
PCT_GL			
PCT_FAST			
PCT_POOL			
SEQ_FLO_1			
DIS			
VEL			
XSLOPE			
XC			
XM			
XG			
XCMG			
C1W_150			
V1W_150			
XFC_LWF			
XFC_SWF			
XFC_TR			
XFC_CL			
XFC_OV			
XFC_UB			
XFC_BO	0.38		
XFC_NAT	-0.26	-0.03	
PFC_LAR	-0.03	0.16	0.41

Appendix S5. Association between local physical habitat variables and the matrices of taxonomic and functional data with forward selection. Codes for variables are listed in Appendix S1. *Variables retained for posterior analyses.

	Taxonomic data						Functional data					
Block of variables	Variables	r^2	Acum r^2	Adj Acum r^2	F	p	Variables	r^2	Acum r^2	Adj Acum r^2	F	p
Channel morphology	XSLOPE	0.17	0.17	0.15	10.31	0.00	XWXD*	0.06	0.06	0.04	3.42	0.00
	XWXD	0.06	0.22	0.19	3.85	0.00	XSLOPE*	0.04	0.11	0.07	2.56	0.02
	XWD_RAT	0.03	0.25	0.21	1.86	0.04						
Substrate	PCT_SA	0.15	0.15	0.13	8.89	0.00	PCT_SA*	0.07	0.07	0.05	3.89	0.00
	PCT_RO	0.05	0.19	0.16	2.88	0.01	PCT_BIGR*	0.06	0.13	0.10	3.71	0.00
	PCT_FL	0.04	0.23	0.19	2.66	0.01	PCT_FL*	0.06	0.19	0.14	3.47	0.00
	PCT_BIGR	0.03	0.27	0.21	2.32	0.02	PCT_CL	0.03	0.22	0.16	2.18	0.04
Channel habitat units	PCT_FAST	0.15	0.15	0.14	9.39	0.00	VEL*	0.08	0.08	0.06	4.30	0.00
	PCT_POOL	0.06	0.21	0.18	3.63	0.00	PCT_POOL*	0.05	0.13	0.10	3.22	0.01
	VEL	0.05	0.26	0.22	3.50	0.00	PCT_FAST*	0.04	0.18	0.13	2.67	0.02
	DIS	0.05	0.31	0.26	3.69	0.00						
Riparian vegetation cover + large woody fragments + instream cover	XFC_LWF	0.18	0.18	0.16	11.38	0.00	XFC_LWF*	0.09	0.09	0.08	5.35	0.00
	XFC_UB	0.11	0.29	0.26	7.74	0.00	XFC_TR	0.06	0.16	0.12	3.90	0.00
	XCMG	0.05	0.34	0.30	4.12	0.00	C1W_150	0.06	0.22	0.17	3.67	0.01
	V1W_150	0.03	0.38	0.32	2.60	0.00						
	XFC_CL	0.03	0.41	0.34	2.45	0.00						
	XFC_SWF	0.02	0.43	0.36	2.03	0.01						
	XC	0.02	0.45	0.37	1.86	0.02						

Appendix S6. Fish species sampled at 54 stream sites in six river basins in the Amazon. AlInv = allochthonous invertivores; AuInv = autochtonous invertivores; Car = carnivores; GInv = general invertivores; Hem = hematofagous; Omn = omnivores; and Per = perifitivores. *Not used in statistical analyses (see main text).

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Beloniformes								
Belonidae								
Potamorrhaphis guianensis (Jardine, 1843)	AlInv	-	1	-	-	-	-	1
Characiformes								
Acestrorhynchidae								
Gnathocharax steindachneri Fowler, 1913	GInv	-	25	-	-	-	-	25
Characidae								
Astyanax gr. *bimaculatus*	Omni	-	-	-	16	-	-	16
Bario steindachneri (Eigenmann, 1893)	Omni		-	2	-	-	-	2
Hemigrammus bellottii (Steindachner, 1882)	AlInv	25	143	83	-	-	-	251
Hemigrammus cf. *pretoensis*	GInv	-	-	-	-	71	-	71
Hemigrammus ocellifer (Steindachner, 1882)	AlInv	7	14	18	-	-	25	64
Hemigrammus schmardae (Steindachner, 1882)	GInv	-	359	-	-	-	16	375
Hemigrammus sp1	GInv	-	-	-	30	-	-	30
Hemigrammus sp2	GInv	-	-	-	-	-	48	48
Hyphessobrycon aff. *melazonatus*	AlInv	-	-	-	-	67	-	67
Hyphessobrycon heterorhabdus (Ulrey, 1894)	GInv	659	452	1925	-	-	5	3041
Jupiaba pirana Zanata, 1997	Omni	-	-	-	1	-	-	1
Knodus sp1	Omni	-	-	-	56	-	-	56
Moenkhausia collettii (Steindachner, 1882)	Omni	-	-	-	-	-	40	40
Moenkhausia comma Eigenmann, 1908	Omni	1	-	-	-	-	-	1
Moenkhausia oligolepis (Günther, 1864)	Omni	-	-	2	19	-	-	21
Priocharax sp1	Omni	-	4	-	-	-	-	4
Pristella maxillaris (Ulrey, 1894)	Omni	-	3	-	-	-	-	3
Crenuchidae								
Ammocryptocharax elegans Weitzman & Kanazawa, 1976	AuInv	3	-	-	-	-	-	3
Characidium cf. *etheostoma*	AuInv	-	-	13	-	-	-	13
Characidium zebra Eigenmann, 1909	AuInv	-	-	-	1	-	-	1
Crenuchus spilurus Günther, 1863	Omni	12	393	-	-	21	1	427
Melanocharacidium cf. *dispilomma*	AuInv	1	-	-	-	-	-	1

Appendix S6. Continuation.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Microcharacidium eleotrioides (Géry, 1960)	AuInv	-	105	-	-	266	-	371
Microcharacidium weitzmani Buckup, 1993	AuInv	758	-	15	-	-	-	773
Poecilocharax weitzmani Géry, 1965	GInv	-	-	-	-	87	-	87
Erythrinidae								
Erythrinus erythrinus (Bloch & Schneider, 1801)	Carn	18	9	170	78	18	7	300
Hoplias malabaricus (Bloch, 1794)	Carn	6	8	9	2	2	-	27
Gasteropelecidae								
Carnegiella strigata (Günther, 1864)	AlInv	3	595	1	-	-	-	599
Iguanodectidae								
Bryconops cf. *caudomaculatus*	GInv	-	-	-	-	1	-	1
Bryconops inpai Knöppel, Junk & Géry, 1968	GInv	-	-	-	-	1	-	1
Bryconops munduruku Silva-Olivera, Canto & Ribeiro, 2015	GInv	-	-	-	-	-	4	4
Bryconops sp1	GInv	-	-	-	-	9	-	9
Iguanodectes rachovii Regan, 1912	Omni	101	5	216	-	-	-	322
Iguanodectes variatus Géry, 1993	Omni	-	-	-	-	-	19	19
Lebiasinidae								
Copella arnoldi (Regan, 1912)	AlInv	415	2476	-	-	-	-	2891
Copella callolepis (Regan, 1912)	Omni	-	24	-	-	-	69	93
Copella nattereri (Steindachner, 1876)	AlInv	-	-	-	-	25	1	26
Lebiasina sp1	Omni	-	-	-	37	-	-	37
Lebiasina sp2	Omni	-	-	-	13	-	-	13
Nannostomus eques Steindachner, 1876	AlInv	-	15	-	-	-	-	15
Nannostomus marginatus Eigenmann, 1909	GInv	-	-	-	-	3	-	3
Nannostomus trifasciatus Steindachner, 1876	AlInv	23	31	13	-	-	-	67
Pyrrhulina aff. *brevis*	AlInv	-	-	337	-	-	-	337
Pyrrhulina brevis Steindachner, 1876	AlInv	-	-	-	-	183	-	183
Pyrrhulina sp1	Omni	-	2	-	-	-	-	2
Pyrrhulina sp2	Omni	47	-	-	-	-	-	47
Cyprinodontiformes								
Cynolebiidae								
Anablepsoides micropus (Steindachner, 1863)	GInv	-	-	-	-	4	-	4
Anablepsoides ornatus (Garman, 1895)	GInv	-	-	-	-	18	-	18
Anablepsoides urophthalmus (Günther, 1866)	AlInv	77	1	44	-	-	-	122
Laimosemion cf. *dibaphus*	GInv	-	-	-	-	-	124	124

Appendix S6. Cont.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Laimosemion strigatus (Regan, 1912)	GInv	75	112	-	-	-	-	187
Melanorivulus cf. *modestus*	Omni	-	-	-	-	-	79	79
Gymnotiformes								
Gymnotidae								
Gymnotus carapo Linnaeus, 1758	GInv	3	-	-	15	-	1	19
Gymnotus cf. *anguillaris*	AuInv	-	-	-	-	-	12	12
Gymnotus coatesi La Monte, 1935	Carn	-	2	-	-	-	-	2
Gymnotus coropinae Hoedeman, 1962	Carn	12	30	76	-	3	2	123
Gymnotus pedanopterus Mago-Leccia, 1994	Carn	-	-	-	-	8	-	8
Gymnotus sp1	GInv	1	-	34	-	-	-	35
Hypopomidae								
Brachyhypopomus beebei (Schultz, 1944)	AuInv	87	-	-	1	-	-	88
Brachyhypopomus brevirostris (Steindachner, 1868)	AuInv	9	12	-	1	-	-	22
Brachyhypopomus bullocki Sullivan & Hopkins, 2009	AuInv	14	-	-	-	-	-	14
Brachyhypopomus sp1	AuInv	2	-	92	-	-	-	94
Microsternarchus bilineatus Fernández-Yépez, 1968	AuInv	4	8	4	-	-	-	16
Rhamphichthyidae								
Gymnorhamphichthys rondoni (Miranda-ribeiro, 1920)	AuInv	59	9	106	-	-	-	174
Hypopygus benoneae Peixoto, Dutra, de Santana & Wosiacki, 2013	AuInv		3	-	-	-	-	3
Hypopygus lepturus Hoedeman, 1962	AuInv	25	13	-	-	-	-	38
Steatogenys elegans (Steindachner, 1880)	AuInv	6	1	-	-	-	-	7
Sternopygidae								
Eigenmannia aff. *trilineata*	AuInv	-	-	-	7	-	-	7
Sternopygus macrurus (Bloch & Schneider, 1801)	Carn	1	-	1	-	-	-	2
Perciformes								
Cichlidae								
Aequidens epae Kullander, 1995	Omni	-	-	-	5	-	-	5
Aequidens pallidus (Heckel, 1840)	Omni	-	-	-	-	104	17	121
Aequidens tetramerus (Heckel, 1840)	Omni	4	8	67	-	-	-	79
Apistogramma gr. *agassizii*	GInv	24	319		-	-	4	347
Apistogramma gr. *regani*	AuInv	444	574	462	-	-	88	1568
Crenicara sp1	AuInv	-	-	2	-	-	-	2
Crenicichla cf. *reticulata*	Carn	1	-	-	-	-	-	1
Crenicichla gr. *saxatilis*	Carn	-	-	30	-	-	-	30

Appendix S6. Cont.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Crenicichla inpa Ploeg, 1991	Carn	-	-	-	1	-	6	7
Crenicichla labrina (Spix & Agassiz, 1831)	Carn	-	2	-	-	-	-	2
Crenicichla sp1	Carn	1	-	-	-	-	-	1
Crenicichla sp2	Carn	-	-	1	-	-	-	1
Nannacara taenia Regan, 1912	AuInv	40	432	-	-	-	-	472
Eleotridae								
Microphilypnus ternetzi Myers, 1927	AuInv	-	2	-	-	-	-	2
Polycentridae								
Monocirrhus polyacanthus Heckel, 1840	Carn	1	4	-	-	-	-	5
Siluriformes								
Aspredinidae								
Bunocephalus coracoideus (Cope, 1874)	GInv	4	-	-	-	-	-	4
Auchenipteridae								
Tetranematichthys wallacei Vari & Ferraris, 2006	Carn	-	1	1	-	-	-	2
Callichthyidae								
Callichthys callichthys (Linnaeus, 1758)	Omni	-	-	2	3	-	-	5
Megalechis picta (Müller & Troschel, 1849)	AuInv	-	-	1	-	-	-	1
Megalechis thoracata (Valenciennes, 1840)	Omni	4	-	-	-	-	-	4
Cetopsidae								
Denticetopsis epa Vari, Ferraris & de Pinna, 2005	Carn	4	-	5	-	-	-	9
Denticetopsis seducta Vari, Ferraris & de Pinna, 2005	Carn	-	-	-	-	1	-	1
Helogenes marmoratus Günther, 1863	AlInv	169	33	152	-	10	59	423
Doradidae								
Acanthodoras cataphractus (Linnaeus, 1758)	Omni	-	1	-	-	-	-	1
Physopyxis ananas Sousa & Rapp Py-Daniel, 2005	Peri	-	132	-	-	-	-	132
Heptapteridae								
Gladioglanis conquistador Lundberg, Bornbusch & Mago-Leccia, 1991	AuInv	85	40	-	-	-	-	125
Pimelodella cristata (Müller & Troschel, 1849)	Omni	-	-	-	1	-	-	1
Pimelodella sp1	Omni	-	-	2	-	-	-	2
Rhamdia quelen (Quoy & Gaimard, 1824)	Carn	1	-	-	-	-	-	1
Loricariidae								
Ancistrus verecundus Fisch-Muller, Cardoso, Silva & Bertaco, 2005	Peri	-	-	-	3	-	-	3
Farlowella amazonum (Günther, 1864)	Peri	4	-	-	-	-	-	4

Appendix S6. Cont.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Rineloricaria cf. *hasemani*	Peri	1	-	-	-	-	-	1
Rineloricaria lanceolata (Günther, 1868)	Peri	-	-	-	-	4	-	4
Pseudopimelodidae		-	-	-	-	-	-	
Batrochoglanis raninus (Valenciennes, 1840)	Carn	1	-	1	-	-	-	2
Trichomycteridae								
Ituglanis amazonicus (Steindachner, 1882)	AuInv	20	-	18	-	-	1	39
Paracanthopoma parva Giltay, 1935*	-	8	-	-	-	-	-	8
Paracanthopoma sp1	Hema	-	-	18	-	-	-	18
Pygidianops amphioxus De Pinna & Kirovsky, 2011*	-	-	-	-	-	17	-	17
Trichomycterus hasemani (Eigenmann, 1914)	AuInv	170	1	3	-	-	-	174
Synbranchiformes								
Synbranchidae								
Synbranchus marmoratus Bloch, 1795*	-	9	3	4	10	6	2	34
Total		**3449**	**6407**	**3930**	**300**	**929**	**630**	**15645**

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Capítulo 3

Are the patterns of different components of Amazon stream fish diversity congruent?

O capítulo III desta tese foi elaborado e formatado conforme as normas da publicação científica *Freshwater Biology*, as quais se encontram em anexo (Anexo 3)

Are the patterns of different components of Amazon stream fish diversity congruent?

Running title: Congruence patterns of fish diversity

Summary

1. The use of a single measure to predict all aspects of diversity has many limitations, because the different components of diversity may show non-congruent patterns. Therefore, the study of multiple components of diversity provide complementary information and can be very useful to several ecological fields.

2. We used data for fish assemblages of 54 streams across six Amazon river basins to examine if nine indices, corresponding to distinct components of diversity (taxonomic diversity, taxonomic distinctness, and functional diversity), are correlated and if they respond to key catchment variables in a similar fashion.

3. We found that many indices are associated, but usually with intermediate correlation. Principal components analyses revealed three significant components of variation. Altitude and slope partially predicted some of the indices.

4. The results indicate that different indices provide complementary information about fish diversity patterns, and that the use of a single component does not provide a comprehensive representation diversity. The catchment variables did not strongly predict most indices, and this suggests that other factors, such as local habitat variables, might have stronger influence on local diversity.

Keywords: taxonomic distinctness; functional diversity; taxonomic diversity; catchment variables; aquatic biodiversity.

Introduction

The great biological diversity in the Neotropics has been a topic of immense interest to ecologist (Magurran & Queiroz, 2010). To quantify biodiversity, the most intuitive measure is to count the number of species in a community (i.e., species richness), but several measures have been developed that also consider the distribution of species relative abundance (Magurran, 2013; Magurran & Queiroz, 2010). Although these indices proved to be very useful, scientists pointed to their limitations, as they account for limited components of biodiversity (Díaz & Cabido, 2001; Stirling & Wilsey, 2001). In recent decades, it has been increasingly recognized that multiple components of diversity should be studied to determine spatial patterns of ecological communities (Meynard et al., 2011; Villéger, Mason, & Mouillot, 2008). In this regard, several studies have incorporated componentes beyond taxonomic diversity, such as functional diversity, to obtain new insights into biological patterns (Almeida et al., 2016; Ernst et al., 2012; Luiza-Andrade, Montag, & Juen, 2017; Meynard et al., 2011; Strecker, Olden, Whittier, & Paukert, 2011).

The functional approach has shown some interesting results. Environmental changes can result in a greater effect on functional diversity than on taxonomic diversity, since environmental filters are expected to act selecting functional traits of species (De Bello et al., 2013; Luiza-Andrade et al., 2017; Pease, Taylor, Winemiller, & King, 2015). Because it can perform differently than its taxonomic counterpart, functional diversity can be used in studies of natural and anthropogenic environmental variation (Villéger, Miranda, Hernández, & Mouillot, 2010). Another measure of diversity deals with taxonomic distinctness based on the relatedness of species, being an approximation of phylogenetic diversity (Clarke & Warwick, 1998; Heino, Mykrä, Hämäläinen, Aroviita, & Muotka, 2007; Heino, Mykrä, & Kotanen, 2008). A diverse community would not only have many species, but also many distinct higher taxa (Gallardo, Gascón, Quintana, & Comín, 2011). Indices of taxonomic distinctness have been applied mostly to detect anthropogenic effects, revealing how modified sites have less diverse species than pristine areas (Munari, Warwick, & Mistri, 2009; Stamou, Polyzou, Karagianni, & Michaloudi, 2017), however, some studies have shown that these indices also respond to natural environmental variation (Alahuhta et al., 2017; Ellingsen, Clarke, Somerfield, & Warwick, 2005). Also, this index has the appealing advantage of being independent to sampling effort, what is desirable for conservation purposes (Clarke & Warwick, 1998; Munari et al., 2009).

For freshwater ecosystems, such as streams, research has demonstrated variable performance of these metrics, with either congruent or non-congruent patterns for different facets of biodiversity. Congruent patterns could indicate that a single index would be sufficient to report variation in biodiversity, saving time and money (Carvalho & Tejerina-Garro, 2015b). On the other hand, a non-congruent pattern means that diversity may be too complex to be described by a single index, and multiple approaches would be required (Devictor et al., 2010). Since one of the goals of ecology is to identify target areas for conservation, it is important to determine if these indices respond in a similar manner to natural environmental variation, especially from large-scale gradients (Heino et al., 2008). Large-scale variables are useful for conservation planning (Heino et al., 2008; Schindler, Von Wehrden, Poirazidis, Wrbka, & Kati, 2013) and are easy to measure using a geographical information system (GIS) in place of expensive field surveys. Moreover, it is well known that stream systems are subjected to hierarchical control, thus, variation in local factors are regulated by variables at catchment-scale, such as altitude and slope (Benone, Esposito, Juen, Pompeu, & Montag, 2017; Frissell, Liss, Warren, & Hurley, 1986). Therefore, large-scale variables might serve as proxies for local-scale environmental variation (Benone et al., 2017) if they show similar relationships variation in stream communities (Jaramillo-Villa, Maldonado-Ocampo, & Escobar, 2010; Lorion, Kennedy, & Braatne, 2011; Sály, Takács, Kiss, Bíró, & Erős, 2011).

In this study, we evaluated multiple indices related to three components of biodiversity of stream fish (taxonomic diversity, taxonomic distinctness and functional diversity) to test for congruent patterns among Amazonian streams. We also assessed the degree to which these índices are similar in their relationships to variation in key catchment variables.

Methods

Study area

We sampled 54 1st to 4th order streams distributed in six river basins: Acará (10 streams), Anapu (10), Capim (10), Juruena (7), Negro (10) and Tapajós (7) River Basins (Figure 1). All streams drain well preserved areas under legal protection, four in public land and two (Acará and Capim) in private areas. The six river basins are distributed across the Amazon rainforest, being primarily covered by rainy forest (Barthem, Charvet-Almeida, Montag, & Lanna, 2004). More details can be found in Benone et al. (2017).

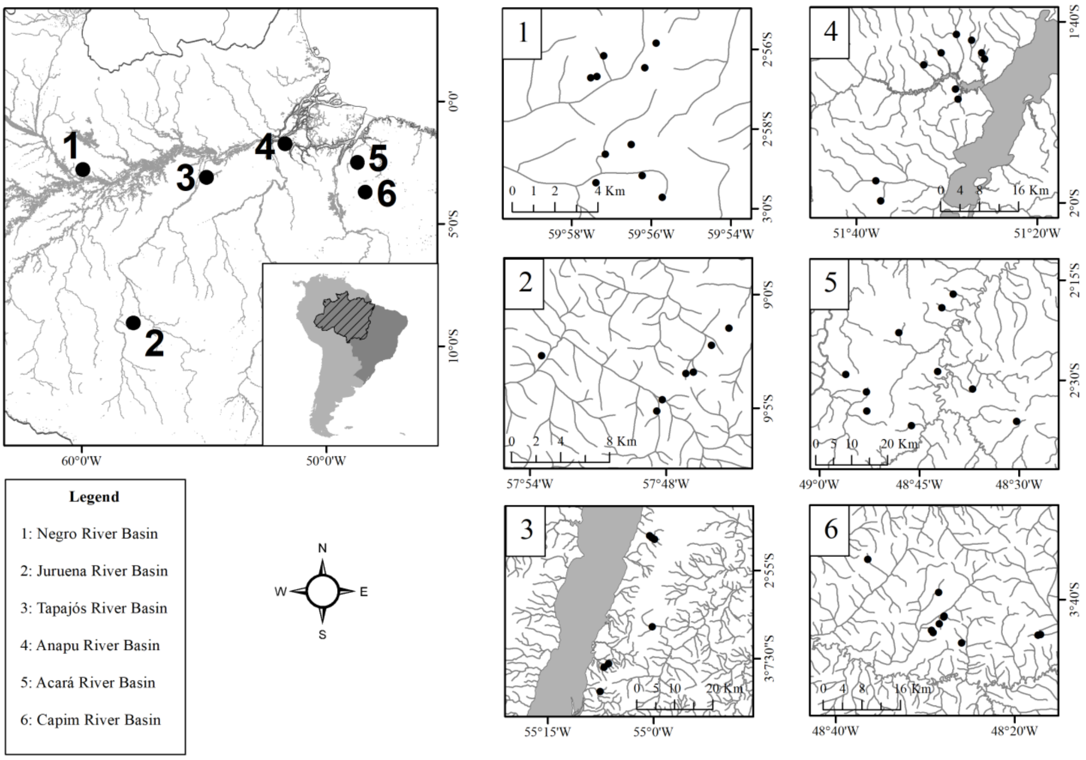

Figure 1. Location of the 54 sampled streams, distributed in six river basins of the Amazon.

Catchment variables

As shown by several studies (Benone et al., 2017; Jaramillo-Villa et al., 2010; Lorion et al., 2011), altitude and catchment slope are important drivers of variation in local physical habitat and in fish diversity of small streams. For the calculation of mean values of these variables for the upstream drainage of each site, we used Shuttle Radar Topography Mission (SRTM) images, obtained at EarthExplorer (http://earthexplorer.usgs.gov/), and the ArcHydro tool within ArcGis software. These two variables were not correlated (Spearman’s r = 0.16).

Fish sampling

Fish specimens were collected using 55-cm diameter hand nets with 2-mm mesh during a six-hour period. This period was equally divided by the ten longitudinal sections and by the number of collectors. Fishes were euthanized with lethal doses of anesthesia (Leary et al., 2013), fixed in 10% formalin, and after 48h, preserved in 70% alcohol. Specimens were identified to the lowest possible taxonomic level using specialized literature complemented by input from specialists. Voucher specimens were deposited in the ichthyological collection of Museu Paraense Emílio Goeldi (MPEG) in Belém, Pará.

Functional traits

We obtained functional traits from five individuals of similar size of each species. For species with sexual dimorphism, we selected only female individuals (Ribeiro, Teresa, & Casatti, 2016). Quantitative traits were chosen based on 16 morphological measures: standard length (SL), maximum body height (MBH), maximum body width (MBW), length of caudal peduncle (LCP), maximum height of caudal peduncle (MHCP), maximum width of caudal peduncle (MWCP), length of pectoral fin (LPF), height of pectoral fin (HPF), height of body midline (HBM), height of eye midline (HEM), head length (HL), head height (HH), mouth width (MW), body area (BA), pectoral fin area (PFA), and mouth orientation (MO) (Ohlberger, Staaks, & Hölker, 2006; Watson & Balon, 1984).

All measures were taken with a digital caliper with 0.1 mm of precision. Body and fins areas were obtained with ImageJ software based on draws of the surface area. These 16 measures were used to obtain 12 ecomorphological indices (Ohlberger et al., 2006; Watson & Balon, 1984) related to vertical position, locomotion and orientation of species (see Table S1 in the Supporting information). In addition, we assigned species into trophic groups (allochthonous invertivores, autochtonous invertivores, carnivores, general invertivores, hematophagus, omnivores, and perifitivores, see Table S2) based on the literature (e. g. Brejão, Gerhard, & Zuanon, 2013; Carvalho & Tejerina-Garro, 2015a; Zuanon et al., 2015). When the information was not available to the species, we extrapolated the data for genus or family level.

Diversity indices

We used nine indices related to taxonomic diversity, taxonomic distinctness, and functional diversity. Three are related to taxonomic diversity (Magurran, 2013): 1) species richness (S); 2) Pielou's evenness (J), a measure of the regularity of species abundance; and 3) Shannon diversity (H'), which summarizes biodiversity based on the number of species and their relative abundances. These indices were calculated using the R function *diversity*.

We also calculated three indices based on taxonomic distinctness, which accounts for the phylogenetic relatedness of species (Clarke & Warwick, 1998, 2001; Magurran, 2013): 4) Taxonomic Diversity (Δ), is the expected path length along a Linnean taxonomic tree between two randomly selected individuals in the sample, weighted by species abundance; 5) Taxonomic Distinctness (Δ^+), a measure of the relatedness of the individual in the sample based on presence-absence data; and 6) Variation in Taxonomic Distinctness (Λ^+), a measure of the evenness of the taxa distribution across the hierarchical taxonomic tree. We used four taxonomic levels (Order, Family, Genus, Species) to calculate the relatedness of pairs of individuals. These indices were calculated using R function *taxondive*.

Finally, we calculated three indices of functional diversity based on multivariate functional trait space (Villéger et al., 2008): 7) Functional Richness (FRic), which is the amount of functional space filled by the community; 8) Functional Evenness (FEve), which describes the regularity of abundances in the functional space; and 9) Functional Divergence (FDiv), representing how abundance is spread within the functional space occupied by the community. For the calculations, all quantitative traits were previously standardized, while qualitative traits were assigned as binary. These indices were calculated using R function *dbFD*.

Statistical analyses

Prior to analyses, all indices and environmental variables were transformed into z-scores. We used correlations among the nine indices of diversity to investigate whether they were congruent. We used Spearman rank correlations, since scatterplot matrices showed that many pairs of indices were not linearly correlated. We also ran a Principal Component Analysis (PCA) to determine if all indices varied similarly, or if more than one axis would be necessary to summarize ecological variation (Wilsey, Chalcraft, Bowles, & Willig, 2005). We applied the broken-stick method to select significant axis.

To determine the response of biodiversity measures to environmental variation, we calculated Spearman rank correlations among the nine indices and the two catchment variables, altitude and slope. We adopted $\alpha = 0.05$, and applied Bonferroni correction for multiple comparisons. All analyses were run in R (R Development Core Team, 2016), with *vegan* (Oksanen et al., 2016), *FD* (Laliberté, Legendre, & Shipley, 2014) and *FactoMineR* (Lê, Josse, & Husson, 2008) packages.

Results

We sampled 15,645 individuals, distributed in seven orders, 26 families and 111 species (Table S2). Three species, *Paracanthopoma parva*, *Pygidianops amphioxus*, and *Synbranchus marmoratus*, were not measured because the former two were too small and the latter is the only species without fins, what could bias our analyses. These three species were excluded from all analyses. Variation of taxonomic distinctness (Λ^+) and functional richness (FRic) showed great variation across streams, while functional evenness (FEve) and functional divergence (FDiv) varied little (Table 1; see Table S3 for individual values per stream). Juruena river basin showed the highest altitudes, and Negro river basin had the steepest slopes (Table 2).

Table 1. Summary of the nine indices of biodiversity of fish from 54 streams sampled across six river basins in the Amazon. SD = standard deviation.

Index	Code	Mean ± SD	Range
Species richness	S	13.46 ± 6.60	4 - 30
Shannon index	H'	1.7 ± 0.41	0.73 - 2.46
Pielou’s evenness	J'	0.69 ± 0.12	0.34 - 0.92
Taxonomic diversity	Δ	80.05 ± 7.05	63.62 - 90.01
Taxonomic distinctness	Δ^+	88.45 ± 4.65	76.8 - 97.65
Variation of taxonomic distinctness	Λ^+	369.33 ± 117.42	77.24 - 572.59
Functional richness	FRic	27.30 ± 28.00	0.10 - 116.76
Functional evenness	FEve	0.74 ± 0.06	0.55 - 0.90
Functional divergence	FDiv	0.69 ± 0.07	0.53 - 0.84

Table 2. Summary of the catchment variables measured in the upstream drainage of 54 streams sampled across six river basins in the Amazon. Values indicate mean ± standard deviation.

River basin	Altitude (m)	Catchment slope (%)
Acará	39.6 ± 8.71	5.38 ± 0.98
Anapu	25.1 ± 5.55	6.85 ± 0.59
Capim	119.6 ± 13.47	5.96 ± 1.05
Juruena	279.71 ± 70.85	10.21 ± 2.58
Negro	72 ± 12.81	11.1 ± 1.1
Tapajós	58.71 ± 29.94	10.68 ± 3.16

Several pairs of indices were correlated (Table 3). For taxonomic diversity indices, both species richness and Pielou’s evenness were correlated with Shannon’s diversity index, but not with each other. All taxonomic distinctness indices were correlated, unlike functional diversity indices, where none were correlated. Species richness, Shannon index and taxonomic diversity were correlated to FRic. FEve and FDiv showed no correlation to any index.

The broken stick method selected the first three axes of PCA (Table 4), which modeled 76.22 % of cumulative variation. Species richness, Shannon’s index, taxonomic diversity and functional richness were positively associated with the first axis. In the second axis, taxonomic distinctness and its variation showed, respectively, a negative and a positive association. Meanwhile, Shannon’s index and Pielou’s evenness were positively correlated with the third axis. Functional evenness and functional divergence were not correlated to any of the selected axes (Figure 2).

Table 3. Pairwise correlations among nine indices of biodiversity of fish from 54 streams sampled across six river basins in the Amazon. Codes for indices are listed in Table 1. Bold values indicate significant correlations at $p < 0.005$ after Bonferroni correction.

	S	H'	J'	Δ	Δ^+	Λ^+	FRic	FEve
H'	**0.71**							
J'	-0.24	**0.41**						
Δ	**0.50**	**0.46**	0.03					
Δ^+	-0.01	-0.07	-0.09	**0.68**				
Λ^+	0.14	0.11	-0.03	**-0.54**	**-0.87**			
FRic	**0.90**	**0.59**	-0.30	**0.49**	0.08	0.10		
FEve	-0.09	0.04	0.11	0.24	0.19	-0.17	-0.20	
FDiv	-0.26	-0.14	0.16	0.11	0.24	-0.22	-0.17	0.18

Table 4. Summary of the Principal Components Analysis (PCA) among the nine indices of biodiversity of fish from 54 streams sampled across six river basins in the Amazon. Bold values indicate strong loadings (≥ 0.60). Codes for indices are listed in Table 1.

	PCA1	PCA2	PCA3
S	**0.85**	0.45	-0.07
H'	**0.63**	0.45	**0.60**
J'	-0.10	0.04	**0.88**
Δ	**0.85**	-0.43	0.14
Δ^+	0.51	**-0.79**	-0.15
Λ^+	-0.28	**0.86**	0.08
FRic	**0.81**	0.37	-0.25
FEve	0.07	-0.28	0.41
FDiv	-0.15	-0.48	0.41
% explanation	31.92	26.70	17.61
% cumulative explanation	31.92	58.62	76.23
Eigenvalues	2.87	2.40	1.58
Broken stick	2.83	1.83	1.33

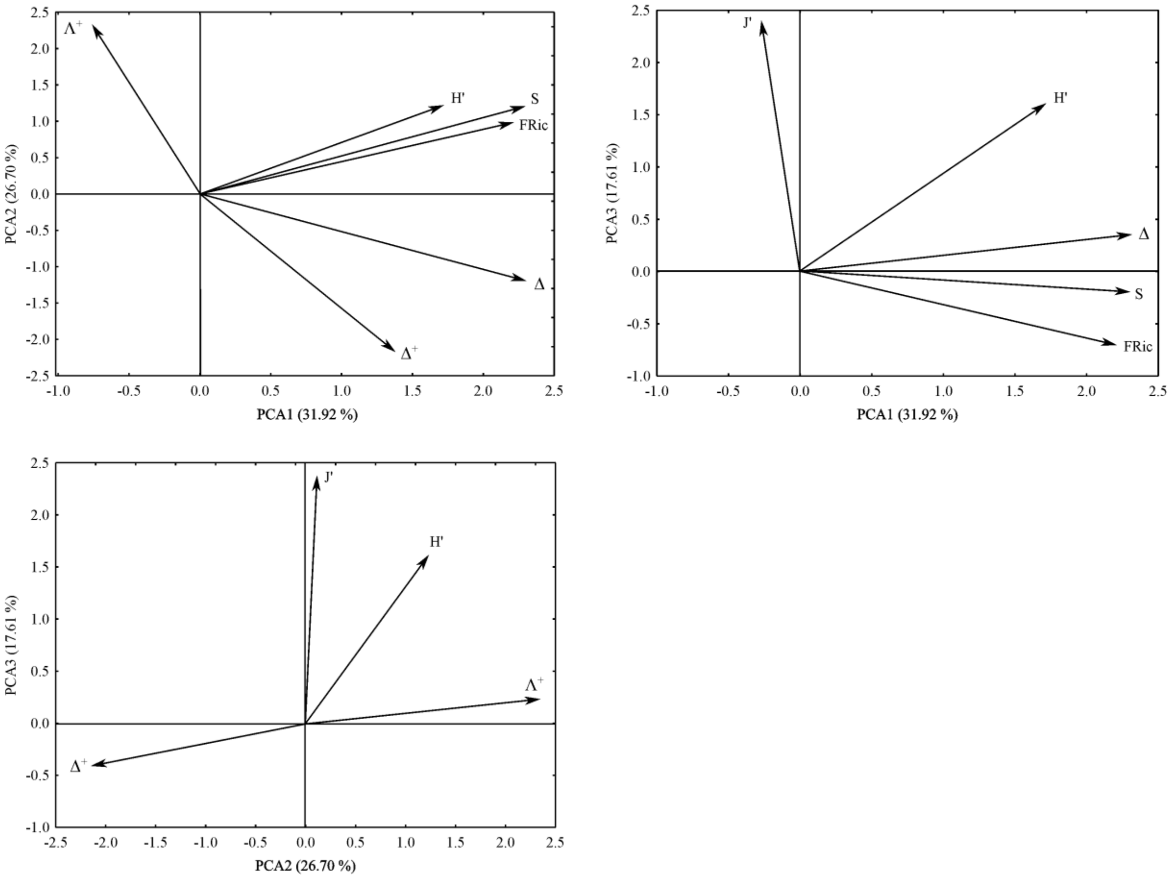

Figure 2. Ordinations of the Principal Components Analysis (PCA) among the nine indices of biodiversity of fish from 54 streams sampled across six river basins in the Amazon. Codes for indices are listed in Table 1.

Species richness and FDiv showed, respectively, negative and positive correlations with altitude, and they were the only indices related to this variable. On the other hand, five indices showed significant correlations with slope. Species richness, Shannon’s index, taxonomic diversity and FRic were negatively affected by slope, whereas Pielou’s evenness was positively associated to this catchment variable. PCA1 showed a negative association with both catchment variables. Taxonomic distinctness, variation of taxonomic distinctness, and FEve showed no response to any explanatory variable (Table 5).

Table 5. Correlations between the nine indices of biodiversity of fish from 54 streams sampled across six river basins in the Amazon and the two catchment variables. Codes for indices are listed in Table 1. Bold values indicate significant correlations at $p < 0.005$ after Bonferroni correction.

	Altitude	**Slope**
S	**-0.49**	**-0.71**
H'	-0.34	**-0.39**
J'	0.13	**0.45**
Δ	-0.23	**-0.43**
Δ^+	0.04	-0.19
Λ^+	-0.03	0.04
FRic	-0.36	**-0.64**
FEve	-0.02	-0.02
FDiv	**0.49**	0.04

Discussion

Our results show a spatial mismatch among the indices, thus supporting the idea that ecological drivers have different effects on distinct components of diversity. With the increasing threats to biodiversity and the reduced funds allocated to conservation strategies, congruent patterns among distinct components of biodiversity is highly desirable, as it can indicate areas that concentrate, simultaneously, high levels of different attributes of diversity. Reports on the patterns of congruence among distinct components of diversity vary in ecological studies. Some detected high correlation among taxonomic, functional and/or phylogenetic diversity (Carvalho & Tejerina-Garro, 2015b; Pool, Grenouillet, & Villéger, 2014; Strecker et al., 2011), reinforcing the idea of using a single measure as a surrogate for diversity. On the other hand, the spatial mismatches observed by Stuart-Smith et al. (2013), De Bello et al. (2013) and Devictor et al. (2010) support the use of a multifaceted framework that provides complementary information for biodiversity assessment.

In recent decades, species richness has been commonly used as the single facet studied in studies investigating biodiversity patterns (Mellin, Bradshaw, Meekan, & Caley, 2010; Oberdorff et al., 2011; Vorste, McElmurray, Bell, Eliason, & Brown, 2017), land-use or climate changes (Hof, Araújo, Jetz, & Rahbek, 2011; Juen et al., 2016; Mantyka-Pringle, Martin, Moffatt, Linke, & Rhodes, 2014), and conservation biology (Abell et al., 2011; Martensen, Ribeiro, Banks-Leite, Prado, & Metzger, 2012). According to Wilsey et al. (2005), these studies make implicit assumptions that richness is highly correlated to other measures of diversity and that it encompasses most of variation in diversity. However, our results emphasize that richness alone cannot summarize all the complexity of ecological variation contained in ecological communities. In addition, three principal components were necessary to describe variations among indices, indicating that each index represents different aspects of diversity, regulated by distinct processes. Similar results were obtained by Wilsey et al. (2005) and Heino et al. (2008). A higher number of ordination dimensions may indicate that indices respond to different environmental gradients, species pools are dissimilar, and/or the dataset involves differences in spatial scale or extent (De Bello et al., 2013; Wilsey et al., 2005).

Large-scale environmental variables are responsible for creating the large-scale gradients that will filter the species pool prior to local factors (De Bello et al., 2013) and lead to strong variation in biodiversity (Schindler et al., 2013). Indeed, altitude and slope predicted the patterns of most indices, albeit many of these correlations were intermediate. Our results revealed that upland streams had lower species richness but increased functional divergence. The decrease in species richness within higher altitudes is a widely acknowledged trend for many groups (De Bello et al., 2013; Heino et al., 2008; Jaramillo-Villa et al., 2010; Lorion et al., 2011), and it may be connected both to environmental filtering and dispersal limitation. The decrease of species richness in latitudinal gradients can be connected to increasing environmental harshness of upland streams. Usually, upland streams have relatively high slopes, cold temperatures, fast water velocity, and less organic substrates (Benone et al., 2017; Jaramillo-Villa et al., 2010; Lorion et al., 2011). However, the lack of association between altitude and slope in the studied streams indicates that changes in fish assemblages may be connected to low immigration rates due to the greater isolation of upland streams (Jaramillo-Villa et al., 2010). Functional divergence is directly linked to niche differentiation (Mason, Mouillot, Lee, & Wilson, 2005; Villéger et al., 2010), thus the higher values of functional divergence in upland streams indicate a higher degree of niche differentiation and functional specialization, while lowland streams have more functionally similar species. This could indicate that biotic interactions may also play a role structuring fish assemblages in upland streams.

Slope influenced several indices of diversity, and low-gradient streams had a more species-rich, functionally-rich and taxonomically-rich fish faunas, but also more uneven distributions of species relative abundance. The enhanced evenness in high-gradient streams might be related to their decreased functional richness and taxonomic diversity (Δ), indicating that fishes in these streams tend to be taxonomically and functionally similar. This could lead to an increase in the importance of biotic interactions, thus enhancing species evenness (Stirling & Wilsey, 2001). On the other hand, Heino et al. (2008) attributed the positive relationship of evenness and slope to the inherent heterogeneity and variability in the conditions of small headwater streams.

Importantly, three indices (Δ^+, Λ^+, and FEve) could not be predicted at all by the chosen variables. We can discard the hypothesis that these indices had low variability, since all of them showed great variation among streams (Table 1 and Table S3). Thus, another possible reason is that there are more significant explanatory variables that were absent in our study. We did not test the influence of local abiotic factors on the indices of diversity, and many studies have shown that they are important to fish assemblages (Rodrigues-Filho, Gurgel-Lourenço, Lima, De Oliveira, & Sánchez-Botero, 2017; Shukla & Bhat, 2017).

The index of taxonomic diversity (Δ) showed the highest number of correlations with other indices, being associated with five other indices. Similar results were reported by Heino et al. (2007) and Heino et al. (2008). This index seems to be a promising tool for ecological studies, as it can be a better proxy for distinct aspects of biodiversity than species richness. Also, the index of taxonomic diversity has the advantage of not being sample-size dependent (Warwick & Clarke, 1995), a desirable quality in assessment programs, which often rely on data with non-standardised sampling effort (Abellán, Bilton, Millán, Sánchez-Fernández, & Ramsay, 2006). Indices of taxonomic distinctness have been suggested to represent anthropogenic-induced changes in ecological communities (Warwick & Clarke, 1995), but studies regarding streams point to its poor performance (Abellán et al., 2006; Alahuhta et al., 2017; Bhat & Magurran, 2006). In addition, some authors found weak to intermediate responses of taxonomic distinctness indices and landscape predictors (Bhat & Magurran, 2006; Heino et al., 2007; Heino et al., 2008), corroborating our results. Hence, the ability of this index to measure variation in biodiversity in natural environmental gradients is relatively unknown for streams, and more information is needed before it applied extensively for biodiversity assessments.

In conclusion, we found that many indices of diversity show partially congruent patterns, but the preponderance of low-intermediate correlations suggests there is a significant level of spatial mismatch among them. Also, the selection of three ordination components indicates that diversity patterns are too complex to be summarized by a single variable. Therefore, we suggest the use of a combination of indices associated with distinct components of diversity to provide complementary information on patterns of fish diversity. Moreover, we found that catchment variables can only partially predict stream fish diversity. This implies that catchment variables alone are not reliable to provide information on stream fish diversity, and that other factors, such as local physical habitat variables, should be included in ecological studies.

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SUPPORTING INFORMATION

Table S1. Ecomorphological indices based on 16 morphological measures. All indices followed Watson and Balon (1984) and Ohlberger, Staaks, and Hölker (2006).

Index	Variable code	Formula	Interpretation
Compression index	CI	MBH/MBW	High values indicate compressed fish which prefer habitats with slow flows
Relative height	RH	MBH/SL	Low values are related to fish inhabiting faster waters and lower capacity of vertical turns
Relative length of caudal peduncle	RLCP	LCP/SL	High values are associated to higher swimming capacity or fishes inhabiting faster waters, but not necessarily nektonic, able to realize propulsion at short distances
Compression index of caudal peduncle	CICP	MHCP/MWCP	Higher values indicate fish with compresses peduncles, typical of fish with slow swimming and low maneuverability
Index of ventral flattening	IVF	HBM/MBH	Lower values indicate fish adapted to fast waters, which can maintain position without swimming, typical of benthic species
Relative area of pectoral fin	RAPF	PFA/BA	High values are related to slow swimming species with good maneuverability or fish adapted to fast waters that live closer to the bottom
Aspect ratio of pectoral fin	ARPF	LPF/HPF	Higher ratios are associated to continuous high-speed swimmers that prefer pelagic regions
Relative length of head	RLH	HL/SL	Fish with larger heads ingest larger preys, thus this index is more related to piscivores
Relative position of eyes	RPE	HEM/HH	High values indicate dorsal eyes, typical of benthic species
Relative width of mouth	RWM	MW/SL	Higher values are associated to fish that ingest larger preys, as piscivorous species
Mouth orientation	MO	°	High values are related to fish that feed closer to the surface. Code: ventral = 0º; inferior = 10 – 80º; terminal = 90º; superior = 100 – 170º
Fineness coefficient	FC	SL/√MBH*MBW	This index evaluates the influence of body shape to swimming efficiency. Values of 2 to 6 indicate reduced drag, optimum ratio is 4.5

Table S2. Fish species sampled at 54 stream sites in six river basins in the Amazon. AlInv = allochthonous invertivores; AuInv = autochtonous invertivores; Car = carnivores; GInv = general invertivores; Hem = hematofagous; Omn = omnivores; and Per = perifitivores. *Not used in statistical analyses (see main text).

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Beloniformes								
Belonidae								
Potamorrhaphis guianensis (Jardine, 1843)	AlInv	-	1	-	-	-	-	1
Characiformes								
Acestrorhynchidae								
Gnathocharax steindachneri Fowler, 1913	GInv	-	25	-	-	-	-	25
Characidae								
Astyanax gr. *bimaculatus*	Omni	-	-	-	16	-	-	16
Bario steindachneri (Eigenmann, 1893)	Omni		-	2	-	-	-	2
Hemigrammus bellottii (Steindachner, 1882)	AlInv	25	143	83	-	-	-	251
Hemigrammus cf. *pretoensis*	GInv	-	-	-	-	71	-	71
Hemigrammus ocellifer (Steindachner, 1882)	AlInv	7	14	18	-	-	25	64
Hemigrammus schmardae (Steindachner, 1882)	GInv	-	359	-	-	-	16	375
Hemigrammus sp1	GInv	-	-	-	30	-	-	30
Hemigrammus sp2	GInv	-	-	-	-	-	48	48
Hyphessobrycon aff. *melazonatus*	AlInv	-	-	-	-	67	-	67
Hyphessobrycon heterorhabdus (Ulrey, 1894)	GInv	659	452	1925	-	-	5	3041
Jupiaba pirana Zanata, 1997	Omni	-	-	-	1	-	-	1
Knodus sp1	Omni	-	-	-	56	-	-	56
Moenkhausia collettii (Steindachner, 1882)	Omni	-	-	-	-	-	40	40
Moenkhausia comma Eigenmann, 1908	Omni	1	-	-	-	-	-	1
Moenkhausia oligolepis (Günther, 1864)	Omni	-	-	2	19	-	-	21
Priocharax sp1	Omni	-	4	-	-	-	-	4
Pristella maxillaris (Ulrey, 1894)	Omni	-	3	-	-	-	-	3
Crenuchidae								
Ammocryptocharax elegans Weitzman & Kanazawa, 1976	AuInv	3	-	-	-	-	-	3
Characidium cf. *etheostoma*	AuInv	-	-	13	-	-	-	13
Characidium zebra Eigenmann, 1909	AuInv	-	-	-	1	-	-	1
Crenuchus spilurus Günther, 1863	Omni	12	393	-	-	21	1	427
Melanocharacidium cf. *dispilomma*	AuInv	1	-	-	-	-	-	1

Table S2. Continuation.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Microcharacidium eleotrioides (Géry, 1960)	AuInv	-	105	-	-	266	-	371
Microcharacidium weitzmani Buckup, 1993	AuInv	758	-	15	-	-	-	773
Poecilocharax weitzmani Géry, 1965	GInv	-	-	-	-	87	-	87
Erythrinidae								
Erythrinus erythrinus (Bloch & Schneider, 1801)	Carn	18	9	170	78	18	7	300
Hoplias malabaricus (Bloch, 1794)	Carn	6	8	9	2	2	-	27
Gasteropelecidae								
Carnegiella strigata (Günther, 1864)	AlInv	3	595	1	-	-	-	599
Iguanodectidae								
Bryconops cf. *caudomaculatus*	GInv	-	-	-	-	1	-	1
Bryconops inpai Knöppel, Junk & Géry, 1968	GInv	-	-	-	-	1	-	1
Bryconops munduruku Silva-Olivera, Canto & Ribeiro, 2015	GInv	-	-	-	-	-	4	4
Bryconops sp1	GInv	-	-	-	-	9	-	9
Iguanodectes rachovii Regan, 1912	Omni	101	5	216	-	-	-	322
Iguanodectes variatus Géry, 1993	Omni	-	-	-	-	-	19	19
Lebiasinidae								
Copella arnoldi (Regan, 1912)	AlInv	415	2476	-	-	-	-	2891
Copella callolepis (Regan, 1912)	Omni	-	24	-	-	-	69	93
Copella nattereri (Steindachner, 1876)	AlInv	-	-	-	-	25	1	26
Lebiasina sp1	Omni	-	-	-	37	-	-	37
Lebiasina sp2	Omni	-	-	-	13	-	-	13
Nannostomus eques Steindachner, 1876	AlInv	-	15	-	-	-	-	15
Nannostomus marginatus Eigenmann, 1909	GInv	-	-	-	-	3	-	3
Nannostomus trifasciatus Steindachner, 1876	AlInv	23	31	13	-	-	-	67
Pyrrhulina aff. *brevis*	AlInv	-	-	337	-	-	-	337
Pyrrhulina brevis Steindachner, 1876	AlInv	-	-	-	-	183	-	183
Pyrrhulina sp1	Omni	-	2	-	-	-	-	2
Pyrrhulina sp2	Omni	47	-	-	-	-	-	47
Cyprinodontiformes								
Cynolebiidae								
Anablepsoides micropus (Steindachner, 1863)	GInv	-	-	-	-	4	-	4
Anablepsoides ornatus (Garman, 1895)	GInv	-	-	-	-	18	-	18
Anablepsoides urophthalmus (Günther, 1866)	AlInv	77	1	44	-	-	-	122
Laimosemion cf. *dibaphus*	GInv	-	-	-	-	-	124	124

Table S2. Cont.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Laimosemion strigatus (Regan, 1912)	GInv	75	112	-	-	-	-	187
Melanorivulus cf. *modestus*	Omni	-	-	-	-	-	79	79
Gymnotiformes								
Gymnotidae								
Gymnotus carapo Linnaeus, 1758	GInv	3	-	-	15	-	1	19
Gymnotus cf. *anguillaris*	AuInv	-	-	-	-	-	12	12
Gymnotus coatesi La Monte, 1935	Carn	-	2	-	-	-	-	2
Gymnotus coropinae Hoedeman, 1962	Carn	12	30	76	-	3	2	123
Gymnotus pedanopterus Mago-Leccia, 1994	Carn	-	-	-	-	8	-	8
Gymnotus sp1	GInv	1	-	34	-	-	-	35
Hypopomidae								
Brachyhypopomus beebei (Schultz, 1944)	AuInv	87	-	-	1	-	-	88
Brachyhypopomus brevirostris (Steindachner, 1868)	AuInv	9	12	-	1	-	-	22
Brachyhypopomus bullocki Sullivan & Hopkins, 2009	AuInv	14	-	-	-	-	-	14
Brachyhypopomus sp1	AuInv	2	-	92	-	-	-	94
Microsternarchus bilineatus Fernández-Yépez, 1968	AuInv	4	8	4	-	-	-	16
Rhamphichthyidae								
Gymnorhamphichthys rondoni (Miranda-ribeiro, 1920)	AuInv	59	9	106	-	-	-	174
Hypopygus benoneae Peixoto, Dutra, de Santana & Wosiacki, 2013	AuInv		3	-	-	-	-	3
Hypopygus lepturus Hoedeman, 1962	AuInv	25	13	-	-	-	-	38
Steatogenys elegans (Steindachner, 1880)	AuInv	6	1	-	-	-	-	7
Sternopygidae								
Eigenmannia aff. *trilineata*	AuInv	-	-	-	7	-	-	7
Sternopygus macrurus (Bloch & Schneider, 1801)	Carn	1	-	1	-	-	-	2
Perciformes								
Cichlidae								
Aequidens epae Kullander, 1995	Omni	-	-	-	5	-	-	5
Aequidens pallidus (Heckel, 1840)	Omni	-	-	-	-	104	17	121
Aequidens tetramerus (Heckel, 1840)	Omni	4	8	67	-	-	-	79
Apistogramma gr. *agassizii*	GInv	24	319		-	-	4	347
Apistogramma gr. *regani*	AuInv	444	574	462	-	-	88	1568
Crenicara sp1	AuInv	-	-	2	-	-	-	2
Crenicichla cf. *reticulata*	Carn	1	-	-	-	-	-	1
Crenicichla gr. *saxatilis*	Carn	-	-	30	-	-	-	30

Table S2. Cont.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Crenicichla inpa Ploeg, 1991	Carn	-	-	-	1	-	6	7
Crenicichla labrina (Spix & Agassiz, 1831)	Carn	-	2	-	-	-	-	2
Crenicichla sp1	Carn	1	-	-	-	-	-	1
Crenicichla sp2	Carn	-	-	1	-	-	-	1
Nannacara taenia Regan, 1912	AuInv	40	432	-	-	-	-	472
Eleotridae								
Microphilypnus ternetzi Myers, 1927	AuInv	-	2	-	-	-	-	2
Polycentridae								
Monocirrhus polyacanthus Heckel, 1840	Carn	1	4	-	-	-	-	5
Siluriformes								
Aspredinidae								
Bunocephalus coracoideus (Cope, 1874)	GInv	4	-	-	-	-	-	4
Auchenipteridae								
Tetranematichthys wallacei Vari & Ferraris, 2006	Carn	-	1	1	-	-	-	2
Callichthyidae								
Callichthys callichthys (Linnaeus, 1758)	Omni	-	-	2	3	-	-	5
Megalechis picta (Müller & Troschel, 1849)	AuInv	-	-	1	-	-	-	1
Megalechis thoracata (Valenciennes, 1840)	Omni	4	-	-	-	-	-	4
Cetopsidae								
Denticetopsis epa Vari, Ferraris & de Pinna, 2005	Carn	4	-	5	-	-	-	9
Denticetopsis seducta Vari, Ferraris & de Pinna, 2005	Carn	-	-	-	-	1	-	1
Helogenes marmoratus Günther, 1863	AlInv	169	33	152	-	10	59	423
Doradidae								
Acanthodoras cataphractus (Linnaeus, 1758)	Omni	-	1	-	-	-	-	1
Physopyxis ananas Sousa & Rapp Py-Daniel, 2005	Peri	-	132	-	-	-	-	132
Heptapteridae								
Gladioglanis conquistador Lundberg, Bornbusch & Mago-Leccia, 1991	AuInv	85	40	-	-	-	-	125
Pimelodella cristata (Müller & Troschel, 1849)	Omni	-	-	-	1	-	-	1
Pimelodella sp1	Omni	-	-	2	-	-	-	2
Rhamdia quelen (Quoy & Gaimard, 1824)	Carn	1	-	-	-	-	-	1
Loricariidae								
Ancistrus verecundus Fisch-Muller, Cardoso, Silva & Bertaco, 2005	Peri	-	-	-	3	-	-	3
Farlowella amazonum (Günther, 1864)	Peri	4	-	-	-	-	-	4

Table S2. Cont.

Taxon/Authority	Trophic guild	Acará	Anapu	Capim	Juruena	Negro	Tapajós	Total
Rineloricaria cf. *hasemani*	Peri	1	-	-	-	-	-	1
Rineloricaria lanceolata (Günther, 1868)	Peri	-	-	-	-	4	-	4
Pseudopimelodidae		-	-	-	-	-	-	
Batrochoglanis raninus (Valenciennes, 1840)	Carn	1	-	1	-	-	-	2
Trichomycteridae								
Ituglanis amazonicus (Steindachner, 1882)	AuInv	20	-	18	-	-	1	39
Paracanthopoma parva Giltay, 1935*	-	8	-	-	-	-	-	8
Paracanthopoma sp1	Hema	-	-	18	-	-	-	18
Pygidianops amphioxus De Pinna & Kirovsky, 2011*	-	-	-	-	-	17	-	17
Trichomycterus hasemani (Eigenmann, 1914)	AuInv	170	1	3	-	-	-	174
Synbranchiformes								
Synbranchidae								
Synbranchus marmoratus Bloch, 1795*	-	9	3	4	10	6	2	34
Total		**3449**	**6407**	**3930**	**300**	**929**	**630**	**15645**

Table S3. Values of the nine indices of diversity for stream fish at each of the 54 streams across six river basins in Amazon. S = species richness; H’ = Shannon index; J’ = Pielou’s evenness; Δ = taxonomic diversity; Δ^+ = taxonomic distinctness; Λ^+ = variation of taxonomic distinctness; FRic = functional richness; FEve = functional evenness; FDiv = functional divergence.

	Basin	S	H’	J’	Δ	Δ^+	Λ^+	FRic	FEve	FDiv
P1F1	Acará	23	2.02	0.64	88.01	91.12	334.80	116.76	0.76	0.59
P2F2	Acará	21	1.91	0.63	84.90	90.55	314.35	105.60	0.70	0.56
P3F3	Acará	18	2.15	0.74	85.45	90.05	362.55	22.98	0.73	0.66
P5F5	Acará	23	2.30	0.73	88.74	91.62	292.23	52.94	0.73	0.69
P6F6	Acará	18	1.74	0.60	86.32	91.39	312.53	29.88	0.81	0.76
P7F7	Acará	18	1.98	0.69	84.54	89.52	328.77	21.71	0.77	0.76
P22F9	Acará	22	2.24	0.72	88.50	90.39	338.13	66.21	0.75	0.62
P23F10	Acará	20	2.07	0.69	87.18	91.43	317.84	28.43	0.70	0.68
P34F12	Acará	19	1.87	0.64	84.48	89.14	426.07	55.93	0.70	0.70
P35F13	Acará	25	2.46	0.76	86.41	89.89	388.48	41.55	0.76	0.69
CAX-D01	Anapu	12	1.74	0.70	70.40	80.09	530.24	11.10	0.79	0.57
CAX-D02	Anapu	19	2.14	0.73	78.95	85.41	450.15	72.93	0.65	0.68
CAX-D03	Anapu	22	2.17	0.70	84.75	89.52	378.87	55.65	0.72	0.62
CAX-D06	Anapu	11	1.65	0.69	76.42	85.01	535.04	7.95	0.74	0.55
CAX-D08	Anapu	21	2.18	0.72	72.74	83.16	572.59	52.98	0.61	0.57
CAX-D09	Anapu	17	1.60	0.56	74.27	81.48	543.67	35.71	0.75	0.58
CAX-D10	Anapu	22	2.04	0.66	85.97	89.05	376.20	67.45	0.71	0.78
CAX-D14	Anapu	22	1.65	0.53	85.68	88.79	407.16	73.49	0.76	0.66
CAX-D15	Anapu	25	1.11	0.34	86.21	90.82	366.62	83.43	0.71	0.61
CAX-D16	Anapu	16	1.96	0.71	76.69	83.59	503.50	16.55	0.80	0.56
IFTREF1	Capim	10	1.56	0.68	82.45	91.54	320.78	18.07	0.78	0.68
IFTREF2	Capim	10	1.38	0.60	81.23	88.49	414.58	15.00	0.76	0.70
IFTREF3	Capim	17	2.30	0.81	88.39	92.36	288.92	44.08	0.82	0.70

Table S3. Continuation.

	Basin	S	H’	J’	Δ	Δ^+	Λ^+	FRic	FEve	FDiv
REF4	Capim	12	1.67	0.67	84.57	92.05	249.15	19.07	0.84	0.77
IFTREF5	Capim	30	2.46	0.72	85.11	89.41	373.17	57.75	0.70	0.69
IFTREF6	Capim	8	0.90	0.43	72.41	90.06	327.25	4.37	0.64	0.79
IFTREF7	Capim	18	2.25	0.78	87.69	90.74	351.47	32.83	0.68	0.78
IFTREF8	Capim	14	2.26	0.86	85.26	90.13	367.03	23.66	0.86	0.77
IFTREF9	Capim	13	1.29	0.50	85.60	92.50	316.84	20.48	0.78	0.77
IFTREF10	Capim	12	1.06	0.43	81.10	91.62	321.55	18.29	0.84	0.79
MT02	Juruena	10	1.91	0.83	69.92	80.74	496.35	7.58	0.69	0.65
MT03	Juruena	6	1.61	0.90	90.01	90.84	380.37	5.60	0.79	0.84
MT04	Juruena	7	1.65	0.85	66.14	80.20	507.77	2.09	0.72	0.73
MT06	Juruena	5	1.29	0.80	63.62	86.26	507.62	14.72	0.65	0.69
MT07	Juruena	9	1.52	0.69	77.35	85.61	476.83	10.57	0.85	0.77
MT09	Juruena	5	0.98	0.61	71.24	86.26	507.62	14.72	0.63	0.75
MT10	Juruena	8	1.35	0.65	73.61	90.06	327.25	16.68	0.56	0.70
DCK01	Negro	8	1.91	0.92	88.99	92.45	209.02	1.72	0.82	0.72
DCK02	Negro	8	1.69	0.81	74.21	86.28	370.95	2.37	0.82	0.59
DCK03	Negro	8	1.77	0.85	77.93	86.28	370.95	6.26	0.91	0.73
DCK04	Negro	6	1.56	0.87	75.67	85.91	297.94	0.99	0.69	0.62
DCK05	Negro	7	1.55	0.80	81.17	89.93	253.35	4.60	0.79	0.79
DCK06	Negro	11	1.37	0.57	66.30	79.18	493.08	6.32	0.74	0.67
DCK07	Negro	10	1.57	0.68	71.81	83.95	543.77	3.56	0.79	0.68
DCK08	Negro	8	1.59	0.76	69.86	78.86	449.57	4.25	0.79	0.73
DCK09	Negro	14	2.02	0.77	81.77	90.86	331.77	43.77	0.74	0.71
DCK10	Negro	9	1.53	0.70	67.32	76.80	456.14	8.90	0.66	0.70

Table S3. Cont.

	Basin	S	H’	J’	Δ	Δ^+	Λ^+	FRic	FEve	FDiv
TPJ02	Tapajós	10	1.66	0.72	83.03	86.06	391.16	7.99	0.79	0.72
TPJ03	Tapajós	7	1.39	0.71	86.98	94.97	152.01	8.21	0.77	0.66
TPJ04	Tapajós	6	1.04	0.58	84.83	97.65	77.24	3.08	0.69	0.63
TPJ05	Tapajós	5	0.73	0.46	78.27	96.48	111.73	1.33	0.82	0.54
TPJ06	Tapajós	4	1.12	0.81	76.96	94.13	172.42	0.10	0.72	0.84
TPJ07	Tapajós	5	1.31	0.81	79.89	96.48	111.73	4.10	0.73	0.73
TPJ08	Tapajós	13	1.71	0.67	75.68	89.16	536.60	21.63	0.73	0.72

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CONCLUSÕES GERAIS

Os resultados desta tese mostraram que os riachos amazônicos apresentam grande heterogeneidade ambiental e uma alta diversidade de espécies, e que variáveis locais, das bacias de drenagens e espaciais são responsáveis pelos padrões de distribuição. No capítulo 1, mostrou-se que as variáveis locais são estruturadas por métricas da bacia, em especial pela altitude e declividade. Tais variáveis afetam a velocidade do fluxo e, com isso, regulam características da morfologia do canal e a proporção e tipo de substratos presentes. No capítulo 2, observou-se que as diversidades alfa taxonômica e funcional foram influenciadas por variáveis locais e espaciais, sem influência de variáveis de bacia. Porém, as diversidades beta taxonômica e funcional foram influenciadas por variáveis espaciais e de bacia. Os resultados mostram forte efeito biogeográfico, no qual as espécies são afetadas por limites à dispersão. A altitude e a declividade foram as principais responsáveis pela diversidade beta, possivelmente por gerarem grandes mudanças no gradiente ambiental. Já mudanças na diversidade alfa estão relacionadas ao tipo de substrato presente nos riachos. Por fim, no capítulo 3, detectou-se que as relações entre os índices foram moderadamente congruentes, bem como suas variações frente às métricas ambientais. Estes resultados indicam que a diversidade de peixes de riachos é complexa demais para ser resumida em um único índice, e um único componente de diversidade não é suficiente para representar a variabilidade natural dessas assembleias. Isso demonstra a importância da utilização de componentes complementares para estudos ecológicos. Além disso, as métricas ambientais estudadas (altitude e declividade) não são preditoras fortes dos padrões de biodiversidade.

Os pequenos riachos são os ecossistemas mais ameaçados frente à crescente degradação dos ambientes naturais, e a avaliação de suas características naturais, bem como sua relação com variáveis de bacia, é imprescindível para futuras medidas de conservação, mitigação de impactos e recuperação de riachos. Os resultados desta tese mostram que os peixes de riachos, ainda pouco estudados considerando a enorme área da Bacia Amazônica, são regidos por mecanismos ecológicos variados e apresentam grande heterogeneidade. A conservação da ictiofauna de riachos depende de abordagens que integrem os diferentes componentes da diversidade e que protejam a bacia como um todo, não apenas riachos individuais. Tal abordagem é essencial tanto para a manutenção da heterogeneidade ambiental em diferentes escalas quanto da grande diversidade de espécies. Considerando-se a importância da Amazônia e dos riachos para a biodiversidade e para a própria vida humana, o estudo e a conservação desses ecossistemas devem ser tomados como medidas prioritárias, do contrário, haverá um aprofundamento das crises da água doce e da biodiversidade.

ANEXO 1

Normas da revista *River Research and Applications,* na qual foi publicado o capítulo I desta Tese. As normas da revista mudaram após a publicação do artigo, portanto, existem algumas inconsistências entre as normas anexadas e o capítulo 1.

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Journal Articles

One author: Fawcett, T. (2006). An introduction to ROC analysis. *Pattern Recognition Letters*, 27(8), 861–874. DOI: 10.1016/j.patrec.2005.10.010.

2 to 7 authors: Daley, C. E., & Nagle, R. J. (1996). Relevance of WISC-III Indicators for assessment of learning disabilities. *Journal of Psychoeducational Assessment*, 14(4), 320–333.

More than 7 authors: Rutter, M., Caspi, A., Fergusson, D., Horwood, L. J., Goodman, R., Maughan, B., … Carroll, J. (2004). Sex differences in developmental reading disability: New findings from 4 epidemiological studies. *Journal of the American Medical Association*, 291(16), 2007–2012. DOI: 10.1001/jama.291.16.2007

In press or forthcoming: van Bergen, E., de Jong, P. F., Maassen, B., Krikhaar, E., Plakas, A., & van der Leij, A. (in press). IQ of four-year-olds who go on to develop dyslexia. *Journal of Learning Disabilities*. DOI: 10.1177/0022219413479673

Books

Personal author(s): Beck, I. (1989). *Reading today and tomorrow: Teachers edition for grades 1 and 2*. Austin, TX: Holt and Co.

Chapter in Edited Book: Borstrøm, I., & Elbro, C. (1997). Prevention of dyslexia in kindergarten: Effects of phoneme awareness training with children of dyslexic parents. In C. Hulme & M. Snowling (Eds.), *Dyslexia: Biology, cognition and intervention* (pp. 235–253). London, UK: Whurr.

Conference Papers

Conference Paper: Balakrishnan, R. (2006, March 25-26). Why aren't we using 3d user interfaces, and will we ever? Paper presented at the IEEE Symposium on 3D User Interfaces. doi:10.1109/VR.2006.148

Conference Proceedings: Rapp, R. (1995). Automatic identification of word translations from unrelated English and German corpora. In *Proceedings of the 37th Annual Conference of the Association for the Computational Linguistics*, pp. 519–525.

Other reference types

Scientific or Technical Reports: NICHD. National Institute of Child Health and Human Development (2000). Report of the National Reading Panel. Teaching children to read: An evidence-based assessment of the scientific research literature on reading and its implications for reading instruction (NIH Publication No. 00-4769). Washington, DC: U.S. Government Printing Office.
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ANEXO 2

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Global Ecology and Biogeography

Edited By: Brian McGill
Impact Factor: 6.045
ISI Journal Citation Reports © Ranking: 2016: 2/49 (Geography Physical); 10/153 (Ecology)
Online ISSN: 1466-8238

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Getting published in *GEB* (also see January 2016 editorial)

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The Journal publishes articles under the following main headers: 1) **Research Papers**, 2) **Ecological Soundings**, 3) **Concepts**, 4) **Meta-analyses**, 5) **Research Reviews**, 6) **Macroecological Methods**, 7) **Data Papers** and 8) **Correspondence**. All submissions are subject to peer review.

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- EMBL Nucleotide Archive: ebi.ac.uk/ena
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2 to 7 authors: Daley, C. E., & Nagle, R. J. (1996). Relevance of WISC-III Indicators for assessment of learning disabilities. *Journal of Psychoeducational Assessment*, 14(4), 320–333.

More than 7 authors: Rutter, M., Caspi, A., Fergusson, D., Horwood, L. J., Goodman, R., Maughan, B., … Carroll, J. (2004). Sex differences in developmental reading disability: New findings from 4 epidemiological studies. *Journal of the American Medical Association*, 291(16), 2007–2012. DOI: 10.1001/jama.291.16.2007

In press or forthcoming: van Bergen, E., de Jong, P. F., Maassen, B., Krikhaar, E., Plakas, A., & van der Leij, A. (in press). IQ of four-year-olds who go on to develop dyslexia. *Journal of Learning Disabilities*. DOI: 10.1177/0022219413479673

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