YURI MALTA CALDEIRA

RIACHOS EM CONDIÇÃO DE REFERÊNCIA EM UMA BACIA NEOTROPICAL:

VARIAÇÃO NATURAL DO HABITAT FÍSICO E SUA INFLUÊNCIA SOBRE A ESTRUTURAÇÃO DA ICTIOFAUNA

LAVRAS – MG
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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestre.

Orientador
Prof. Dr. Paulo dos Santos Pompeu

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Profa. Dra. Carla Rodrigues Ribas UFLA

Profa. Dra. Letícia Maria Vieira UFSJ

Prof. Dr. Paulo dos Santos Pompeu
Orientador

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“Viver é muito perigoso…”

Riobaldo Tatarana

RESUMO

Áreas em condição de referência são locais onde as relações bióticas e abióticas de um ecossistema mais se assemelham às relações naturais na ausência de interferência antrópica. A caracterização física e biótica das áreas em condição de referência estabelece bases de comparação essenciais para avaliação, manejo e recuperação de ecossistemas. Apesar de ser tema bem desenvolvido em países temperados, o estudo de áreas em condição de referência para ecossistemas de água doce ainda é um tema incipiente para região tropical que, ironicamente, abriga grande parte da biodiversidade aquática continental. A defasagem quanto ao conhecimento sobre condições de referência é especialmente alarmante para países tropicais em desenvolvimento como o Brasil, onde o impacto do setor econômico primário sobre os ecossistemas aquáticos é elevado. Dessa maneira, nós amostramos o habitat físico e a ictiofauna de 31 riachos em condição de referência na bacia do rio São Francisco, no estado brasileiro de Minas Gerais, a fim de entender a variação espacial natural do habitat físico e sua relação com a estruturação das assembléias de peixes. Nós amostramos 255 métricas de habitat físico para cada riacho e um total 4297 peixes de 50 espécies diferentes foi regsitrado. As condições naturais do habitat físico dos riachos foram dependentes da posição geográfica dos mesmos: quanto maior a proximidade, maior a semelhança entre as condições. Entre riachos próximos, a similaridade entre as condições naturais de substrato, abrigo para peixes e vegetação ripária, e as de química da água e morfologia do canal foi positivamente relacionada à similaridade da elevação média e da vazão dos mesmos, respectivamente. Por sua vez, a maior parte (51%) da variação natural da composição das assembléias de peixe foi explicada pela posição geográfica (27%), frequência de corredeiras (14%), heterogeneidade de fluxo (6%) e abundância de madeira para abrigo para peixe (5%) dos riachos em condição de referência. A relevância da posição geográfica para explicação da variação natural das condições do habitat físico e da composição das assembléias de peixe reflete a influência de características da paisagem sobre os riachos e ressalta a necessidade de estabelecer conjuntos de áreas de referência regionais para a bacia do rio São Francisco. Além disso, observou-se que características físicas do habitat local relacionadas a adaptações morfológicas dos peixes são igualmente importantes às da paisagem para estruturação da ictiofauna. Esses resultados são a primeira contribuição para o estudo de riachos em condição de referência em bacias Neotropicais e apontam a necessidade de atuação em diferentes escalas espaciais para a maior eficiência da conservação desses ecossistemas.

Palavras-chave: Áreas de referência. Habitat físico. Ictiofauna. Estruturação de comunidades. Riachos.

ABSTRACT

Reference condition areas are ecosystems in which the biotic and abiotic relationships are most similar to their natural conditions in the absence of human interference. The physical and biotic characterization of reference condition areas sets essential standards for assessment, management, and recovery of ecosystems. Despite being a well-developed subject in temperate countries, the study of reference condition areas for freshwater ecosystems is incipient in the tropical region which ironically holds a great part of freshwater biodiversity. The lack of knowledge on reference conditions is especially alarming for developing tropical countries such as Brazil where there is a large impact of the primary sector of the economy on freshwater ecosystems. Thus, we assessed the physical habitat conditions and the ichthyofaunal composition of 31 reference condition streams in the São Francisco river baisn, in the Brazilian state of Minas Gerais, in order to understand the natural spatial variation of the physical habitat and its relationship with the structuring of fish assemblages in a Neotropical river basin. We sampled 255 physical habitat metrics in each stream and a total of 4297 fishes of 50 different species was registered. The natural physical habitat conditions of the streams depended on their geographic position: streams located near to each other had more similar conditions. Mean elevation and water flow were positively related to the natural condition of substrate, fish shelter and riparian vegetation, and water chemistry and channel morphology of streams in a same region, respectively. Additionally, most (51%) of the natural variation of the composition of fish assemblages was explained by the geographic position (27%), frequency of riffles (14%), flow heterogeneity (6%), and abundance of woody fish shelter (5%) of reference condition streams. The relevance of geographic position for the explanation of the natural variation of physical habitat conditions and compositions of fish assemblages reflects the influence of landscape characteristics on streams. It also indicates that regional rather than basin-sclae reference conditions are more appropriate for the São Francisco river basin. Furthermore, we observed that local physical habitat characteristics related morphological adaptations of fishes are equally important as landscape chracteristics for the structuring of fish assemblages of sterams. The present results are the first contribution to the study of reference condition streams in a Neotropical river basin. They indicate the necessity of acting at different spatial scales to promote better conservation strategies for Neotropical freshwater ecosystems.

Keywords: Reference condition areas. Physical habitat. Ichthyofauna. Community structuring. Streams.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO

A presente dissertação é parte do projeto intitulado "*O papel dos parques nacionais na conservação de peixes de riachos da bacia do São Francisco em Minas Gerais: definindo estratégias para conservação da ictiofauna*" que contou com financiamento da Fundação Grupo Boticário de Proteção à Natureza. O objetivo desse projeto é verificar a eficiência dos parques nacionais no auxílio à conservação da ictiofauna conhecida de córregos de pequeno porte da bacia do rio São Francisco, em Minas Gerais. A realização desse projeto contribui para o preenchimento da lacuna de conhecimento a respeito da estrutura da ictiofauna de riachos tropicais em áreas protegidas e da efetividade destas para proteção desses ecossistemas.

Nesse contexto, eu discorri a respeito da variação natural do habitat físico de riachos da bacia do rio São Francisco e a forma como ela influencia a diversidade beta da ictiofauna na região. Os parques nacionais são algumas das áreas com menor interferência humana na bacia do rio São Francisco e por isso as condições dos ecossistemas nelas presentes foram consideradas como referência no que diz respeito à manutenção das relações ecológicas naturais. A partir desse pressuposto, eu investiguei, no primeiro capítulo desta dissertação, a variação natural do habitat físico de riachos tropicais pela mensuração e posterior comparação de diversas métricas de habitat físico dos riachos dos parques nacionais da bacia do rio São Francisco. Ainda no primeiro capítulo, eu determinei quais características físicas mais contribuíram para a diferenciação do habitat de riachos em condições com mínima interferência humana. O conhecimento sobre a variação natural de características físicas do habitat de riacho tropicais apresentado é escasso, apesar de sua grande relevância para a preservação de ecossistemas aquáticos tropicais.

No segundo capítulo, eu abordei a relação entre a variação natural do habitat físico de riachos tropicais e a variação na composição das assembleias de peixe entre riachos. Os habitats aquático e terrestre têm grande influência sobre a fauna aquática de riachos e podem ser analisados em diferentes escalas geográficas. Assim, eu analisei as características físicas mais relevantes para estruturação da comunidade de peixes em riachos de referência na bacia do rio São Francisco. Primeiramente, eu identifiquei as características físicas do habitat que mais contribuíram para a dissimilaridade da composição das assembleias de peixe. Posteriormente, eu determinei as principais espécies relacionadas às características físicas mais relevantes. Finalmente, eu observei uma congruência entre as discrepâncias do habitat e da fauna de peixes entre riachos. A partir disso, eu discuti como, em condições naturais, as características físicas do habitat possivelmente influenciaram a composição das assembleias de peixe de riacho tropicais em diferentes escalas espaciais. Os resultados desse capítulo suprem a carência de informações quanto à variação natural da ictiofauna em riachos neotropicais e suas potenciais relações com o habitat físico, contribuindo para a preservação da elevada diversidade aquática tropical.

2 REFERENCIAL TEÓRICO

O termo “áreas em condição de referência” foi desenvolvido para designar ecossistemas cujas condições bióticas e abióticas serviriam de parâmetro de boa qualidade para fins de estudo, manejo e conservação de ecossistemas alterados (HUGHES; LARSEN; OMERNIK, 1986). Inicialmente, o termo foi utilizado exclusivamente para designar ecossistemas pristinos, mas a carência de áreas sem qualquer interferência humana na maioria das regiões do planeta levou à flexibilização do mesmo (STODDARD et al., 2006). Atualmente, o termo “áreas em condição de referência” indica os ecossistemas menos perturbados e cujas relações e processos naturais mais se aproximam das condições na ausência de interferência antrópica para determinada região (HAWKINS; OLSON; HIL, 2010; BAILEY; LINKE; YATES, 2014). Em países desenvolvidos, estudos sobre condições de referência são comumente utilizados por agências de proteção ambiental e são elaborados principalmente para ambientes de água doce (KERSHNER et al., 2004; PEDERSEN; KRISTENSEN; FRIBERG, 2014; DOLL et al., 2015).

Ecossistemas de água doce são afetados tanto por condições do ambiente aquático quanto terrestre (BARTELS et al., 2012). Além disso, grande parte da biodiversidade do planeta é encontrada nos ecossistemas aquáticos continentais (BALIAN et al., 2008) e a heterogeneidade de habitat nesses ambientes é um dos principais fatores que promovem essa elevada riqueza de espécies. Assim, a demanda humana por recursos naturais aquáticos e as alterações do uso do solo são algumas das principais ameaças à integridade biótica dos corpos d’água e sua grande biodiversidade (SALA et al., 2000). O impacto sobre os ecossistemas aquáticos continentais é mais notório na região tropical. Países tropicais em desenvolvimento abrigam a maior parte da diversidade de peixes de água doce do planeta (LÉVÊQUE et al., 2008), mas sua economia baseada principalmente na exploração direta dos recursos naturais (e.g. agropecuária, silvicultura, mineração) é uma grande ameaça às espécies aquáticas devido às alterações do habitat físico promovidas por essas atividades econômicas (AGOSTINHO; THOMAZ; GOMES, 2005).

O habitat físico está intimamente relacionado à estruturação das comunidades bióticas aquáticas (WEINLÄNDER; FÜREDER, 2012; FEIO et al., 2015). Características inerentes aos corpos d'água tais como substrato do leito e tipo de fluxo determinam os tipos de abrigo disponíveis e favorecem a estrutura morfológica de determinadas espécies. Além disso, características terrestres associadas aos ambientes aquáticos como a estrutura da vegetação ripária, por exemplo, determinam a qualidade do material alóctone que é fornecido aos organismos aquáticos e controlam a quantidade de energia solar que é fornecida para a produção primária autóctone (JACKSON; PERES-NETO; OLDEN, 2001). Dessa maneira, a compreensão da condição natural do habita físico dos ambientes aquáticos é essencial para a conservação desses ecossistemas (RICHTER et al., 1997). Logo, a maior parte dos estudos sobre áreas em condição de referência envolve um levantamento minucioso e padronizado de características físicas do habitat relacionadas a morfologia do canal, vegetação ripária, abrigo para organismos aquáticos, substrato, química da água e tipos de fluxo (KAUFMANN et al., 1999; CALLISTO et al., 2002; PARSONS; THOMS; NORRIS, 2004). Além da carcacterização do habitat físico, os estudos das áreas em condição de referência geralmente envolvem a análise da estruturação de comunidades de um ou mais grupos de organismos.

O conhecimento sobre a relação entre a estruturação de comunidades e as condições do habitat físico dos ecossistemas aquáticos fornece subsídios para a criação de ferramentas de diagnóstico de alteração e recuperação ambiental (KIM; AN, 2015). As comunidades bióticas são compostas por espécies cujas respostas às condições ambientais variam quanto a qualidade e intensidade. Dessa forma, alterações em alguma das condições ambientais tem o potencial de promover alterações na riqueza e equitabilidade das comunidades (KOSNICKI et al., 2014). Logo, o conhecimento sobre as relações naturais em áreas em condição de referência garante maior eficiência no diagnóstico das alterações do habitat físico e seu impacto sobre a estrutura da comunidade alvo (WHITE; WALKER, 1997). Dentre os organismos, macroinvertebrados são alguns dos mais utilizados na caracterização de ambientes aquáticos (FERREIRA et al., 2014; MILNER et al., 2015) devido a sua alta sensibilidade e tempo de resposta curto a variações das condições ambientais. Porém, os peixes também são muito utilizados devido a sua grande mobilidade, plasticidade trófica inter-específica e apelo público que garantem respostas a variações espacialmente amplas, respostas que atingem diferentes níveis tróficos e maior apoio público aos estudos, respectivamente (HEINO et al., 2015).

O Brasil é o país com uma das maiores diversidades de peixes de água doce e concentra muitas das maiores bacias hidrográficas do planeta (LATRUBESSE; STEVAUX; SINHA, 2005). Contraditoriamente, o conhecimento sobre as condições naturais do habitat físico dos ecossistemas de água doce brasileiros e sua relação com a estruturação das comunidades de peixes é incipiente. Apesar da existência de legislação específica para a proteção dos recursos hídricos brasileiros (BRASIL, 1997), a eficiência de conservação da integridade dos ecossistemas aquáticos é baixa devido, entre outros motivos, à falta de embasamento científico das diretrizes. Os critérios e parâmetros foram estabelecidos desconsiderando áreas em condição de referência e a variação espacial natural dos ambientes, sendo criadas normas fixas para toda a extensão do território brasileiro. Dessa maneira, a integridade biótica de importantes bacias hidrográficas é prejudicada pela grande pressão antrópica e pela falta de uma estratégia de conservação eficiente (FERREIRA et al., 2012). A maior bacia hidrográfica localizada inteiramente em território brasileiro, a bacia do rio São Francisco (GODINHO; GODINHO, 2003), é uma delas. Um total de 208 espécies nativas de peixe já foi registrado para a bacia (ALVES; VIERIA; POMPEU, 2011) e seus trechos alto e médio abrigam grandes áreas do bioma Cerrado, um hotspot de biodiversidade (MYERS et al., 2000). Ainda assim, a porção da bacia localizada no estado de Minas Gerais encontra-se bastante alterada por atividades agropecuárias e de mineração (AZZONI, 2001), sendo que os ecossistemas em melhores condições estão localizados nas unidades de proteção integral (e.g. parques nacionais).

O presente estudo contemplou a análise da variação do habitat físico e sua relação com a estruturação das assembleias de peixes de riachos em condição de referência em cinco parques nacionais da bacia do rio São Francisco, em Minas Gerais. O objetivo foi contribuir para maior eficiência da conservação das bacias hidrográficas Neotropicais a partir da compreensão das relações e variações naturais em ecossistemas em condição de referência. No primeiro artigo, eu analisei a variação espacial do habitat físico e testei o quanto dessa variação podia ser explicado pela posição geográfica, elevação e vazão médias dos riachos em condição de referência. No segundo capítulo, eu analisei a variação na estrutura das assembleias de peixes entre riachos e identifiquei as espécies que mais contribuíram para diferenciação entre grupos de riachos com assembleias similares. Ainda no segundo capítulo, eu testei quanto da variação da estruturação das assembleias de peixes foi explicado por características da paisagem e do habitat físico local, e identifiquei as características locais que melhor explicaram essa variação.

3 CONSIDERAÇÕES FINAIS

Eu pude concluir que as condições do habitat físico de riachos de uma bacia hidrográfica Neotropical apresentaram ampla variação espacial e influenciaram a estruturação da ictiofauna com magnitude similar nas escalas local e de paisagem. Os resultados do primeiro capítulo demonstraram que as condições do habitat físico dos riachos em condição de referência na bacia do Rio São Francisco apresentaram ampla variação natural, principalmente no espaço e localmente em relação à elevação e vazão médias. Eu sugiro que valores de referência para variáveis físicas do habitat de riachos em regiões com ampla diversidade ambiental (e.g. regiões tropicais) devem ser definidas para escalas geográficas reduzidas (e.g. sub-bacias) e, se possível, para riachos com elevação e vazão semelhantes. No segundo capítulo, eu demonstrei que a maior parte da diferenciação natural das assembleias de peixe em riachos em condição de referência na bacia do Rio São Francisco é explicada por características físicas do habitat nas escalas da paisagem e local em proporções similares. Além disso, eu identifiquei que, na escala local, variações de fluxo de água e complexidade de habitat são as principais relacionadas às diferenças entre assembleias de peixe. A partir disso, foi possível inferir a respeito de características do habitat relacionadas à elevada diversidade beta de peixes de ecossistemas aquáticos em regiões com elevada diversidade ambiental (e.g. riachos tropicais). Este é o primeiro estudo sobre riachos em condição de referência em uma bacia Neotropical e mostra que as estratégias de conservação para esses ecossistemas aquáticos podem ser mais eficientes se atuarem em diferentes escalas espaciais e utilizarem áreas de referência próximas e com vazão e elvação médias similares as da área de estudo. Logo, os resultados da presente dissertação sobre a variação natural do habitat físico de riachos na bacia do Rio São Francisco e sua relação com a diversidade da ictiofauna dessa bacia são uma nova contribuição científica com potencial para o manejo e a conservação de ecossistemas aquáticos tropicais.

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SEGUNDA PARTE – ARTIGOS

ARTIGO 1

Natural variation of physical-habitat conditions among reference streams of a Neotropical river basin in Brazil

Yuri Malta Caldeira[1,2]; Ruanny Casarim[1]; Paulo dos Santos Pompeu[1]

[1] Setor de Ecologia Aplicada, Departamento de Biologia, Universidade Federal de Lavras, Av. Doutor Sylvio Menicucci 1001, Lavras, Brazil

[2] Correspondent author's e-mail: yurimc86@gmail.com

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Abstract

The determination of the natural variation of physical habitat conditions of ecosystems is the first step toward the establishment of reference standards which are important for fauna and habitat conservation. Tropical regions hold most of global freshwater diversity, nevertheless little is known about the natural conditions of physical habitats that promoted and support such diversity. We sampled and calculated 255 physical habitat metrics for 31 streams in five protected areas of the Brazilian São Francisco river basin in order to identify the most variable natural characteristics among tropical streams in reference condition areas. We performed principal components analyses (PCA) that indicated the most relevant metrics for ordination of streams in each of the following categories: water chemistry (2); substrate (7); fish shelter (6); riparian vegetation (9); channel morphology (7). We used ditance-based linear models (DISTLM) to test how much of the variation of the metrics in each category could be explained by geographic position, average elevation, and average water flow of streams. The best statistically significant models explained 42% of substrate (33% geographic position; 9% average elevation), 26% of channel morphology (22% geographic position; 4% average water flow), 23% of water chemistry (14% geographic position; 9% average water flow), 17% of fish shelter (9% geographic position; 8% average elevation), and 14% of riparian vegetation (7% geographic position; 7% average elevation) variation. Thus, regional features (e.g. geology and climate) related to the geographic position are of greater importance, followed by average elevation and discharge for determining physical habitat characteristics of tropical streams. Therefore, we suggest that reference sites should be set for tropical streams in the same regional landscape and, preferably, with similar average elevation and discharge.

Keywords: Reference condition; habitat characteristics; habitat spatial structure; tropical streams; lotic ecosystem

Resumo

A determinação da variação natural das condições do habitat físico de ecossistemas é o primeiro passo para o estabelecimento de padrões de referência que são importantes para a conservação da fauna e do habitat. Regiões tropicais possuem grande parte diversidade de água doce do mundo, ainda assim pouco se sabe sobre as condições naturais do habita físico que originaram e apoiam essa diversidade. Nós amostramos e calculamos 255 métricas de habitat físico para 31 riachos em cinco áreas protegidas bacia hidrográfica brasileira do rio São Francisco a fim de identificar as características naturais que mais variam entre riachos tropicais de áreas em condição de referência. Nós realizamos análises de componentes principais (*PCA*) que indicaram as métricas mais relevantes para a ordenação dos riachos em cada uma das seguintes categorias: química da água (2); substrato (7); abrigo para peixe (6); vegetação ripária (9); morfologia do canal (7). Nós utilizamos modelos lineares baseados em distância (*DISTLM*) para testar quanto da variação das métricas em cada categoria poderia ser explicada pela posição geográfica, elevação média e vazão média dos trechos dos riachos. Os melhores modelos estatisticamente significantes explicaram 42% da variação de substrato (33% posição geográfica; 9% elevação média), 26% de morfologia do canal (22% posição geográfica; 4% vazão média), 23% de química da água (14% posição geográfica; 9% vazão média) e 14% de vegetação ripária (7% posição geográfica; 7% elevação média). Logo, aspectos regionais (e.g. geologia e clima) relacionados à posição geográfica dos trechos dos riachos são de maior importância para determinação características físicas do habitat de riachos tropicais, seguidos em importância pela elevação média e descarga dos trechos. Assim, nós sugerimos que locais de referência devem ser estabelecidos para riachos tropicais numa mesma paisagem regional e, preferencialmente, com elevação e descarga médias similares.

Palavras-chave: Condição de referência; características do habitat; estruturação especial do habitat; riachos tropicais; ecossitema lótico

Introduction

The definition of goals and reference standards are a basic premise of ecosystems conservation (Nestler *et al*. 2010; Laub *et al*. 2012; Dedieu *et al*. 2015). The determination of "reference conditions" is one way to meet that assumption. The Reference Condition Approach (RCA) is the general denomination of the group of methods used to set standard values for preserved natural environments and that can potentially be used to quantify impacts and establish goals for similar but altered environments (Hughes *et al*. 1986). Although RCA is broadly used in habitat assessment protocols of environmental agencies around the world, the definition of "reference condition" is still controversial (Hawkins *et al*. 2010; Bailey *et al*. 2014). Some researchers will argue the term "reference condition" should be used exclusively for pristine environments while others defend its use also for minimally and least disturbed sites once pristine environments are rare in most regions (Stoddard *et al*. 2006; Lisle *et al*. 2007; Kosnicki *et al*. 2014). Another controversy involving RCA is the definition of an appropriate geographic scale for habitat assessment studies (Wang *et al*. 2006). A large scale approach may be desirable for state- or baisn-scale management but it might prevent the differentiation between "reference" and impacted sites due to naturally variable "reference conditions" in heterogeneous environments (White & Walker 1997). Therefore, some authors defend that habitat assessments involving the RCA should be conducted over a regional spatial scale (Hughes *et al*. 1986; Stoddard *et al*. 2006).

Physical habitat characteristics are an important part of habitat assessment protocols. Most habitat quality assessments involve some method of measuring physical habitat metrics although precision and refinement may vary among methods (Bain *et al*. 1999). Independent of accuracy, measurements of physical habitat parameters are relevant because they are intimately associated with organisms and work as indicators of ecosystem health (Weinländer & Füreder 2012; Al-Shami *et al*. 2013; Feio *et al*. 2015; Kim & An 2015). Substrate, temperature, and geomorphology are examples of commonly assessed habitat characteristics in freshwater ecosystems (Collins *et al*. 2011; Imholt *et al*. 2013; Civas *et al*. 2016). In those ecosystems, physical habitat conditions are especially suceptiable to the impact of human alterations because they are affected by both waterbody and land use (Richter *et al*. 1997). Thus, it is not surprising that many habitat assessment protocols were developed to assess and manage the condition of freshwater ecosystems (Kaufmann *et al*. 1999; Callisto *et al*. 2002; Parsons *et al*. 2004).

Freshwater ecosystems house a large portion of worlds biodiversity and also contribute for the support of terrestrial life (Balian *et al*. 2008; Bartels *et al*. 2012). The biodiversity of freshwater ecosystems is directly linked to the physical habitat heterogeneity of waterbodies. Thus, the usage of freshwater by human activities and its susceptibility to indirect effects of land use threaten and disrupt freshwater ecosystems (Sala *et al*. 2000). Among those imperiled ecosystems, streams deserve especial attention: they comprise the largest areas of most watersheds; hold many endemic species; are sensitive to terrestrial impacts; and impacts on streams potentially propagate downstream (Vannote *et al*. 1980; Ward 1989; Hoagstrom *et al*. 2011; Múrria *et al*. 2015). In temperate regions, there are several examples of stream habitat assessment and management based on the RCA (Kershner *et al*. 2004; Pedersen *et al*. 2014; Doll *et al*. 2015). Thus, some temperate countries take action to study and protect those ecosystems (e.g. Europe's Water Framework Directive). On the other hand, most tropical countries still lack efficient water management programs despite their multiple freshwater habitat and biological diversity.

The role of Brazil as one of the leading exporters of agricultural products in the world takes a toll on its natural resources (Morton *et al*. 2006; Carvalho *et al*. 2009). Furthemore, the country has poor environmental management practices (Ferreira *et al*. 2012), especially regarding freshwater environments. The brazilian water policy (Lei nº 9.433/1997) was a first step toward freshwater conservation, but many of the proposed measures still lack implementation (Sparovek *et al*. 2010). Additionally, the efficiency of protected areas for freshwater preservation have rarely been assessed and knowledge on national "reference condition" waterbodies is absent.

Here we assess the physical habitat conditions of 31 streams in five protected areas of the Brazilian São Francisco river basin, and briefly discuss the matter of geographic resolution in RCA studies based on our data. For this study, we considered protected areas of the upper São Francisco river basin as reference sites based on them being the least impacted habitats in this region. Then, we present the natural variance of physical habitat conditions for the reference streams in this region and offer potential explanations for differences in relevant characteristics among streams.

Material and methods

Study area

The São Francisco river basin drains an area of 645067.2 km^2 and it is the largest basin entirely located in Brazil (Godinho & Godinho 2003). The São Francisco river runs through five states and the upper and part of middle regions of its basin occupy approximately 40 % of Minas Gerais state area. Cerrado and Caatinga are the predominant biomes in São Francisco river basin (Alves & Leal 2010). In Minas Gerais, Cerrado is predominant in the upper region of the basin while in the middle it is the transition between Cerrado and Caatinga. A total of 493723.27 ha are protected by five national parks (PARNA) in Minas Gerais: Serra da Canastra, Serra do Cipó, Sempre-Vivas, Grande Sertão Veredas, and Cavernas do Peruaçu. 'National park' is one of the protected areas categories with most restrictive use in Brazilian legislation (SNUC 2000), thus national parks are some of the best-preserved natural areas in Brazil.

Serra da Canastra National Park is located in southwestern Minas Gerais and has an area of 197787 ha. This park was established in 1972 and constitutes one of the main federal areas for the protection of the Cerrado (MMA/IBAMA 2005a). The park and its surrounding area encompass 581.7 km^2 of the São Francisco river basin.

Serra do Cipó National Park is located in central Minas Gerais and has an area of 31617.8 ha. This park was established in 1984 (MMA/ICMBio 2009) and protects areas of Cerrado and Atlantic Forest. The Espinhaço Complex mountain range runs across the park and separates the drainage of the São Francisco river from the Brazilian East Atlantic costal drainages (Alves et al 2008). The park area includes almost all the headwaters of the Cipó river which is one of the best-preserved tributaries of one of the largest rivers that run to the São Francisco river in its upper region.

Sempre-Vivas' National Park is located in the northern center of Minas Gerais and has an area of 124154.47 ha. This park was established in 2002 and protects Cerrado and Atlantic Forest areas. The Espinhaço Complex mountain range runs across the park and separates the São Francisco river drainage from the Jequitinhonha river drainage in this region (MMA/ICMBio 2014).

Grande Sertão Veredas National Park is located in northern Minas Gerais and has an area of 83364 ha. This park was established in 1989 and contemplates six different Cerrado physiognomies. The region of the park holds a great amount of water in the soil due to the predominance of arenites among the sediments. The water bodies in the park belong to the Carinhanha and Urucuia rivers basins, important tributaries on the left margin of the São Francisco river (MMA/IBAMA & FUNATURA 2003).

Cavernas do Peruaçu National Park is located in northern Minas Gerais and has an area of 56800 ha. This park was established in 1999 and protects a transitional area between Cerrado and Caatinga. The Peruaçu river is the main water body in the park. This river is an important tributary of the São Francisco river due to its perennial flow in a region of dry climate. Karstic formations are common in the Peruaçu river basin due to the water erosion of carbonate rocks of the Bambuí Group (MMA/IBAMA 2005b).

Data sampling

We sampled 31 second or third order streams (Strahler 1957) inside the five national parks previously mentioned. From September to October of 2014, we sampled seven streams in PARNA Serra do Cipó and nine in PARNA Serra da Canastra. In April of 2015, we sampled one stream in PARNA Cavernas do Peruaçu, eight in PARNA Grande Sertão Veredas, and four in PARNA Sempre-Vivas. We returned to PARNA Sempre-Vivas in October 2015 and sampled two additional streams. All sampling occurred during the dry season which is considered the best period for stream characterization (Kaufmann et al. 1999). The scarcity of rain in 2014 and 2015 reduced the number of streams with flowing water during the dry season though. Therefore, we selected streams based on the presence of water and our capacity to access them.

We sampled streams following the methods described by Peck *et al*. (2006) and Hughes and Peck (2008). We delimitated a 150 m long reach at each stream and divided it in ten 15 m long transects using 11 cross-sections. We took depths measurements and evaluated the presence of fine sediment at ten equally distant points along each transect. We visually determined the type of flow at each transect point and counted the number of channel bars, wood debris in the bankfull stage channel, lateral channels, and backwater pools along the transect. We used a compass and estimated the percentage length of the reach running in each direction to determine changes in flow direction and sinuosity.

We characterized the habitat of the stream channel and riparian zones at each cross-section. We first measured the depth and visually determined the type of substrate and its immersion at five points equally distant along the cross-section. We measured the canopy cover over the channel and banks using a convex spherical densiometer (Lemmon 1957). We visually determined and quantified the abundance of potential fish shelters (algae, macrophytes, wood debris, tree roots, leaf banks, overhanging vegetation, undercut banks, boulders, artificial structures) 5 m upstream and downstream from each cross-section. We measured bank angle with a clinometer and used a measuring tape for undercut banks length, channel wetted width, channel bars width, channel height and width at bankfull stage, and channel incision height. We characterized the riparian vegetation based on a 10-m^2 quadrat on each bank. The quadrats extended 5 m upstream and 5 m downstream from the cross-section and we visually estimated the percentage cover of each type of vegetation for the canopy layer, understory, and ground cover layer. We also visually identified potential human impacts (e.g. pasture, agriculture, and mining) in the area and estimated their distance from the banks. We used a GPS to obtain the elevation, latitude, and longitude of the points at the ends of the reach and used the difference in elevation to calculate reach slope. We also used elevation data from both ends of each reach to calculate its mean elevation. Latitude and longitude of the upstream-end of the reach were combined to determine the geographic position of the reach.

We measured water chemistry parameters at the end or beginning of the reach before sampling other physical habitat metrics. We used a multiparameter water quality probe to measure water pH, conductivity, temperature, and dissolved oxygen. We took measurements right below water surface at the center point of the cross-section of the stream.

Data analysis

We calculated 255 physical habitat related metrics from the field sampling data following Peck *et al*. (2006) and Hughes and Peck (2008). We used the data from the field to produce 36 substrate metrics, 35 fish shelter metrics, 101 riparian vegetation metrics, 48 channel morphology metrics, 29 human impact metrics, and six water chemistry metrics (S1). Out of this 255 metrics, we selected eight for substrate, eight for fish shelter, 14 for riparian vegetation, 17 for channel morphology, and four for water chemistry based on the results of correlation analyses between metrics (one metric excluded when correlation was statistically significant and the coefficient greater than 75%) and the recurrence of metrics (or equivalent metrics) in different habitat assessment protocols. We excluded human impact metrics from analyses because we were only interested on the natural variations of the physical habitat of streams and human interference inside national parks was generally restricted to low-impact tourism (e.g. trails).

We performed PCA analyses for each of the metrics category to identify the most important metrics for the ordination of samples. We used the software Statistica v. 10 (Stat Soft 2011) to run the PCA analyses and summarize all the metrics in each of the five categories into two or three principal components. We used the scores of principal components with eigenvalue greater than one to create 2-dimensional scatterplots. We added the average elevation of the samples to the scatterplots as a bubble variable and colored each of the samples according to the parks in which they are located. We analyzed the scatterplots to evaluate potential correlations between metrics, mean elevation, and geographic position of streams.

We used distance-based linear models (DISTLM) to test how much of the natural variability of the physical habitat conditions could be explained by geographic, elevational, and hydraulic features. We used the software Primer+Permanova (Clarke & Gorley 2006) to perform a DISTLM analysis for each of the categories using the habitat metrics as response variables and stream mean elevation, geographic position, and water flow as explanatory variables. Water flow rate was calculated from the sampled data. We grouped streams latitude and longitude in the explanatory matrix to represent streams' geographic position. We chose Euclidean distance as the similarity index for the matrix due to the exclusively environmental nature of our data. We used the forward selection of models and adopted a 0.05% significance value. The best model was the one with greater adjusted-R^2 among the statistically significant.

RESULTS

Physical habitat conditions presented great variation among reference streams along the upper and middle São Francisco river basin in Minas Gerais (S1). Geographic position, mean elevation, and water flow rate of reference streams explained part of the variation of physical habitat profiles of streams. 'Geographic position' was the most important explanatory variable. It explained most of the variation in water chemistry (14%), substrate (33%), fish shelter (9%), riparian vegetation (7%), and channel morphology (22%) of streams. 'Mean elevation' had minor importance explaining the variation in substrate (9%) and fish shelter (8%), and the same importance as geographic position in the case of riparian vegetation (7%). 'Water flow' had minor importance explaining the variation in water chemistry (9%) and channel morphology (4%).

Water chemistry

Four water chemistry metrics resulted in a single principal component. PCA principal component represented 50% of water chemistry related variation among streams. The principal component represented the absolute and relative amounts of dissolved oxygen in water, and the most important metrics for its ordination were ‘dissolved oxygen concentration’ and ‘percent dissolved oxygen’.

Geographic position and water flow of stream reaches explained part of the variation in water chemistry conditions among streams. ‘Geographic position’ explained 21% of variation in water chemistry among streams by itself. The best statistically significant model (adjusted R^2 = 0.23; P = 0.02) explained 23% of variation in water chemistry among streams (Table 1) and included ‘geographic position’ and ‘water flow’ as predictor variables. In this model, geographic position alone explained 14% of the variation and water flow added 9% of explanation power to it. ‘Mean elevation’ did not contribute to the explanation of water chemistry variation.

Table 1. Relationship between the variation physical habitat conditions and geographic position, mean elevation, and water flow of reference streams. The best model for the Distance-based Linear Model (DISTLM) analysis is presented for each category of variables.

Variables	**Adjusted R^2**	**Pseudo-F**	**P-value**
Water chemistry			
Geographic position	0.14	3.45	<0.01
+ Water flow	0.23	3.87	0.02
Substrate			
Geographic position	0.33	8.52	<0.01
+ Mean elevation	0.42	5.27	<0.01
Fish shelter			
Geographic position	0.09	2.55	0.01
+ Mean elevation	0.17	3.51	0.02
Riparian vegetation			
Mean elevation	0.07	3.34	0.02
+ Geographic position	0.14	2.06	0.04
Channel morphology			
Geographic position	0.22	5.26	<0.01
+ Water flow	0.26	2.52	0.03

Substrate

Eight substrate metrics were represented in two principal components. PCA principal components 1 and 2 represented 62 and 17% of substrate related variation among streams, respectively (Figure 1). The first principal component represented the abundance and embeddedness of large sediment, and the most important metrics for its ordination were ‘mean substrate size’, ‘percentage of substrate > 16 mm diameter’, ‘percentage of small sediment on channel bed’, ‘percentage of channel’s substrate average immersion’, and ‘relative bed stability (Log10)’. The second principal component represented the abundance of small sediment, and the most important metrics for its ordination were ‘percentage of substrate < 16 mm diameter’ and ‘percentage of sand and fine sediment’.

The qualitative analysis of the PCA plot (Figure 1) suggested an association between geographic position, elevation, and substrate profile of stream reaches. Most stream reaches in the upper region of the São Francisco river basin (southern and center MG) were represented in the upper left quadrat and were at higher elevation while most stream reaches in the middle region of the São Francisco river basin (northern MG) were represented in the upper right quadrat and lower center of the plot. This suggests that reference streams at higher elevation have more stable beds with bigger substrate while reference streams at lower elevation have predominance of small substrate with natural greater embeddedness. Actually, average sediment size in the channel decreased with reference streams’ elevation above sea level: higher elevation (1023.5 to 1365 m) streams had predominance of rock bottoms and boulders; medium elevation (800 to 984 m) streams had predominance of boulders and cobble; and lower elevation (580 to 790.5 m) streams had predominance of sand and fine sediment (Figure 2).

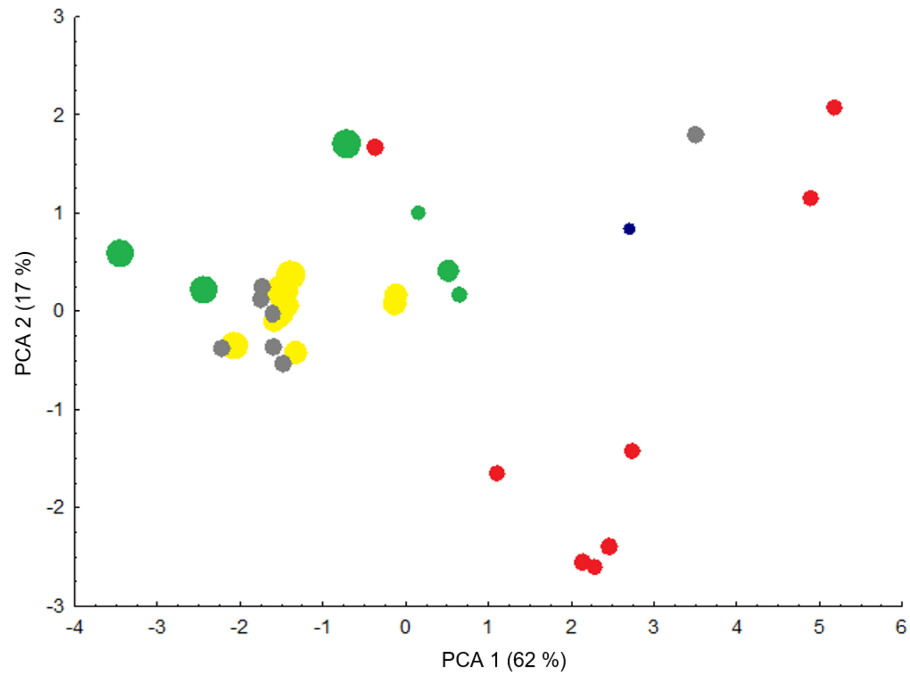

Figure 1. Ordination of reference streams based on the variation of most relevant streambed substrate characteristics. Mean elevation of stream reaches is directly proportional to the diameter of the circles. The color of the circles indicates the National Park in which reaches are located: blue = Cavernas do Peruaçu National Park; green = Sempre-Vivas National Park; grey = Serra do Cipó National Park; red= Grande Sertão Veredas National Park; yellow = Serra da Canastra National Park.

Geographic position and mean elevation of stream reaches explained part of the variation of streambed substrate (Table 1) as inferred from the PCA plot (Figure 2). The variables 'geographic position' and 'mean elevation' by themselves explained 27 and 22% of variation in substrate profile among streams, respectively. Moreover, the best statistically significant model (adjusted R^2 = 0.42; $P < 0.01$) explained 42% of variation in substrate profile among streams and included 'geographic position' and 'mean elevation' as predictor variables. In the model, 'geographic position' alone explained 33% of the variation and 'mean elevation' added 9% of explanation power to it. 'Water flow' did not contribute to the explanation of substrate profile variation.

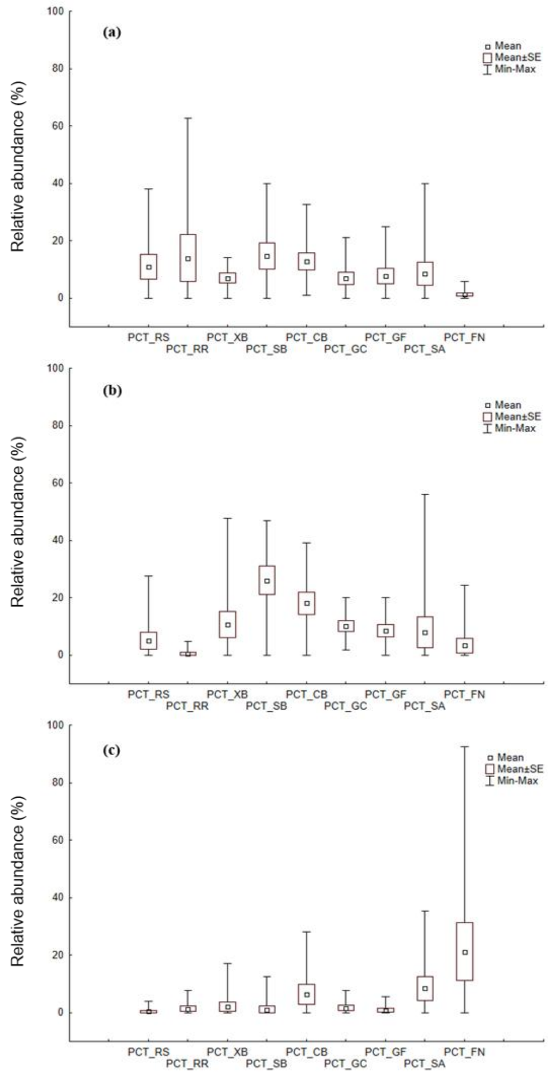

Figure 2. Average sediment size in the channel of **(a)** higher elevation (1023.5 to 1365 m) streams; **(b)** medium elevation (800 to 984 m) streams and **(c)** lower elevation (580 to 790.5 m) streams. PCT_RS – percentage of smooth bedrock (> 4000mm); PCT_RR – percentage of rough bedrock (> 4000 mm); PCT_XB – percentage of large boulders (1000 to 4000 mm); PCT_SB – percentage of small boulders (250 to 1000 mm); PCT_CB – percentage of cobble (64 to 250 mm); PCT_GC – percentage of coarse gravel (16 to 64 mm); PCT_GF – percentage of fine gravel (2 to 16 mm); PCT_SA – percentage of sand (0.6 to 2 mm); PCT_FN – percentage of fine sediment (< 0.6 mm).

Fish shelter

Eight fish shelter metrics resulted in two principal components. PCA principal components 1 and 2 represented 42 and 24% of fish shelter related variation among streams, respectively (Figure 3). The first principal component represented the abundance of total fish shelter and tree related fish shelter, and the most important metrics for its ordination were ‘total areal cover for fish except filamentous algae and aquatic macrophytes’, ‘large and small woody debris areal cover’, ‘leaf bank areal cover’, and ‘root areal cover’. The second principal component represented the abundance of macrophytes and algae, and the most important metrics for its ordination were ‘filamentous algae and aquatic macrophyte areal cover’, and ‘aquatic macrophyte areal cover’.

The qualitative analysis of the PCA plot (Figure 3) suggested no association between geographic position, elevation, and fish shelter abundance. Stream reaches geographically distant from each other and with great elevation difference appeared close together in the PCA plot. This suggests fish shelter abundance in reference streams in the São Francisco iver basin is independent of geographic position and elevation of the stream reach.

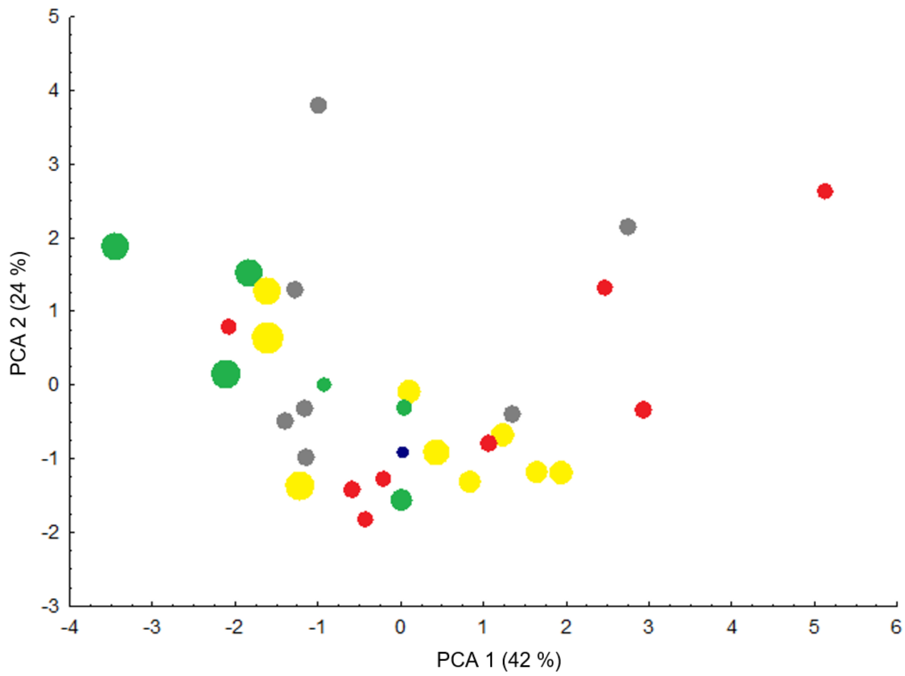

Figure 3. Ordination of reference streams based on the variation of most relevant fish shelter characteristics. Mean elevation of stream reaches is directly proportional to the diameter of the circles. The color of the circles indicates the National Park in which reaches are located: blue = Cavernas do Peruaçu National Park; green = Sempre-Vivas National Park; grey = Serra do Cipó National Park; red= Grande Sertão Veredas National Park; yellow = Serra da Canastra National Park.

Geographic position and mean elevation and geographic position of stream reaches explained part of the variation of fish shelter abundance (Table 1). The best statistically significant model (adjusted $R^2 = 0.17$; $P = 0.02$) explained 17% of variation in fish shelter abundance among streams and included ‘geographic position’ and ‘mean elevation’ as predictor variables. In the model, ‘geographic position’ explained 9% of the variation and ‘mean elevation’ added 8% of explanation power to it. ‘Water flow’ did not contribute to the explanation of the variation of fish shelter abundance.

Riparian vegetation

Fourteen riparian vegetation metrics resulted in three principal components. PCA principal components 1, 2, and 3 represented 52, 21, and 8% of riparian vegetation related variation among streams, respectively (Figure 4). The first principal component represented the density of tree trunks and wood debris, and the most important metrics for its ordination were ‘density of large wood debris in and above active channel – size class 3’, ‘density of large wood debris above active channel – size class 1’, ‘density of large wood debris above active channel – size class 3’, ‘density of large wood debris above active channel – size class 2’, and ‘density of large wood debris above active channel- size class 2’. The second principal component represented the density of canopy cover over the stream and the riparian zone, and the most important metrics for its ordination were ‘riparian canopy and mid-layer cover’, ‘mean percentage of canopy density mid-stream’, and ‘mean percentage of canopy density at bank’. The third principal component represented the average ground cover of the riparian zone, and the most important metric for its ordination was ‘riparian ground-layer vegetation cover’.

The qualitative analysis of the plot which axis represent principal components 1 and 2 of the PCA (Figure 4) suggested an association between geographic position, mean elevation, and riparian vegetation profile of stream reaches. Most stream reaches in the upper region of the São Francisco river basin (southern and center MG) were represented in the lower and center left of the plot and presented higher elevation and most stream reaches in the middle region of the São Francisco river basin (northern MG) were represented in the upper center of the plot. This suggests that reference streams at lower elevation have taller riparian vegetation with more woody plants than reference streams at higher elevation.

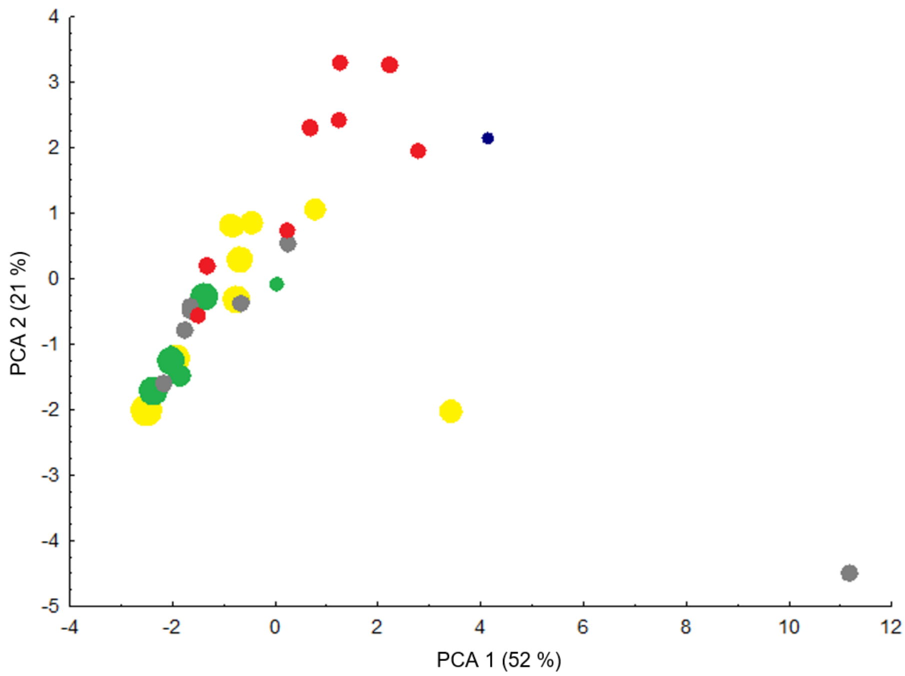

Figure 4. Ordination of reference streams based on the variation of most relevant characteristics related to the riparian vegetation. Mean elevation of stream reaches is directly proportional to the diameter of the circles. The color of the circles indicates the National Park in which reaches are located: blue = Cavernas do Peruaçu National Park; green = Sempre-Vivas National Park; grey = Serra do Cipó National Park; red= Grande Sertão Veredas National Park; yellow = Serra da Canastra National Park.

Geographic position and mean elevation explained part of the variation of riparian vegetation related characteristics (Table 1) suggested by the PCA plot for the streams (Figure 5). The variables ‘geographic position’ and ‘mean elevation’ by themselves explained 13 and 10% of variation in riparian vegetation profile among streams, respectively. Moreover, the best statistically significant model (adjusted R^2 = 0.14; P = 0.04) explained 14% of variation in riparian vegetation profile among streams and included ‘geographic position’ and ‘elevation’ as predictor variables. In the model, ‘geographic position’ alone explained 7% of the variation and ‘elevation’ added 7% of explanation power to it. ‘Water flow’ did not contribute to the explanation of the variation of riparian vegetation related characteristics. Wood debris density was lower for national parks where sampled stream reaches had higher mean elevation (Figure 5). Serra da Canastra National Park and Sempre-Vivas National Park had low density of wood debris and high reach mean elevation. Serra do Cipó National Park had medium density of wood debris and medium reach mean elevation. Grande Sertão Veredas National Park had high density of wood debris and low mean reach elevation

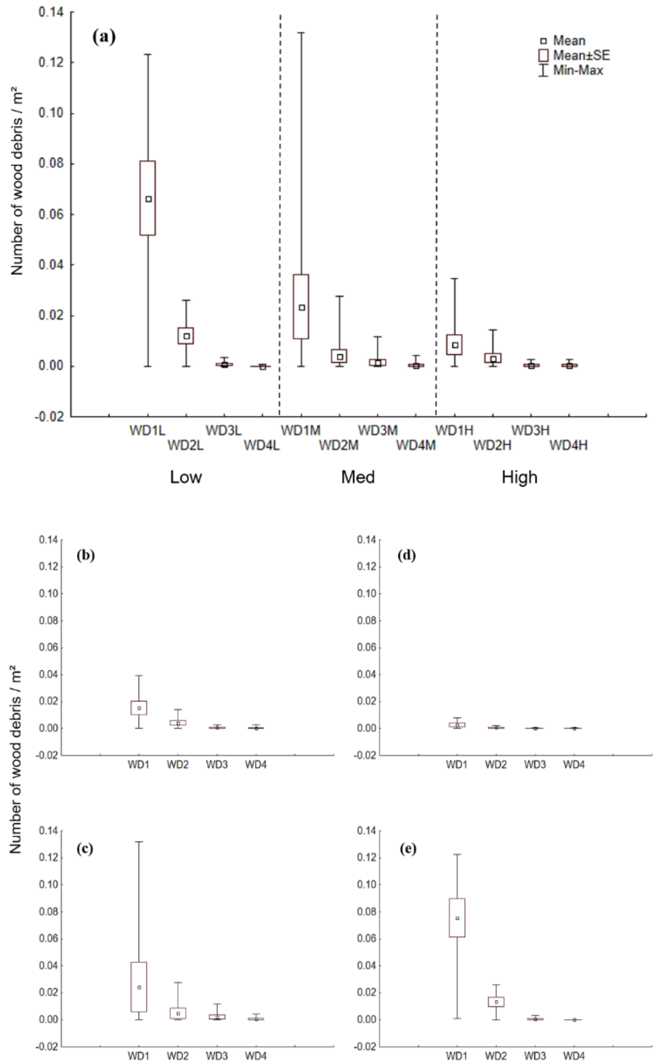

Figure 5. (a) Density of wood debris from riparian vegetation for low (580 to 790.5 m), Medium (800 to 984 m) and high (1023.5 to 1365 m) mean elevation streams, and (b) for Serra da Canastra National Park**,** (c) Serra do Cipó National Park, (d) Sempre-Vivas National Park**,** and (e) Grande Sertão Veredas National Park. WD1 – wood very small to very large; WD2 – wood small to very large; WD3 – wood medium to very large; WD4 – wood large to very large. L – low mean elevation; M – medium mean elevation; H – high mean elevation.

Channel morphology

Ten channel morphology metrics resulted in three principal components. PCA principal components 1, 2, and 3 represented 40, 17, and 16% of channel morphology related variation among streams, respectively (Figure 6, Figure 7). The first principal component represented the frequency of flow types, and the most important metrics for its ordination were ‘percent riffle’, ‘percent falls, cascade, rapids, and riffles’, and ‘percent glides and all pool types’. The second principal component represented the frequency of variation between flow types, and the most important metrics for its ordination were ‘fast and slow flow water flow sequence’ and ‘water flow heterogeneity (fast, smooth, and pool sequence)’. The third principal component represented the average velocity and reach sinuosity, and the most important metrics for its ordination were ‘mean water velocity’ and ‘channel sinuosity’.

The qualitative analysis of the PCA plots (Figure 6 and 7) suggested an association between geographic position, mean elevation, and channel morphology of stream reaches. Stream reaches in the upper region of the São Francisco river basin (southern and center MG) were represented scattered along the left half and stream reaches in the middle region of the São Francisco river basin (northern MG) were represented along the horizontal mid-section of Figure 4. This suggests that reference streams in the upper region present greater alternation between fast and slow water flows. Most stream reaches in the upper region of the São Francisco river basin were represented in the upper left quadrat of Figure 5 and presented higher elevation. Five stream reaches in the middle region of the São Francisco river basin were represented in the center right half and other four were scattered in the left half of Figure 5. This suggests that reference streams in the upper region of the basin are generally sinuous with slow and smooth flow.

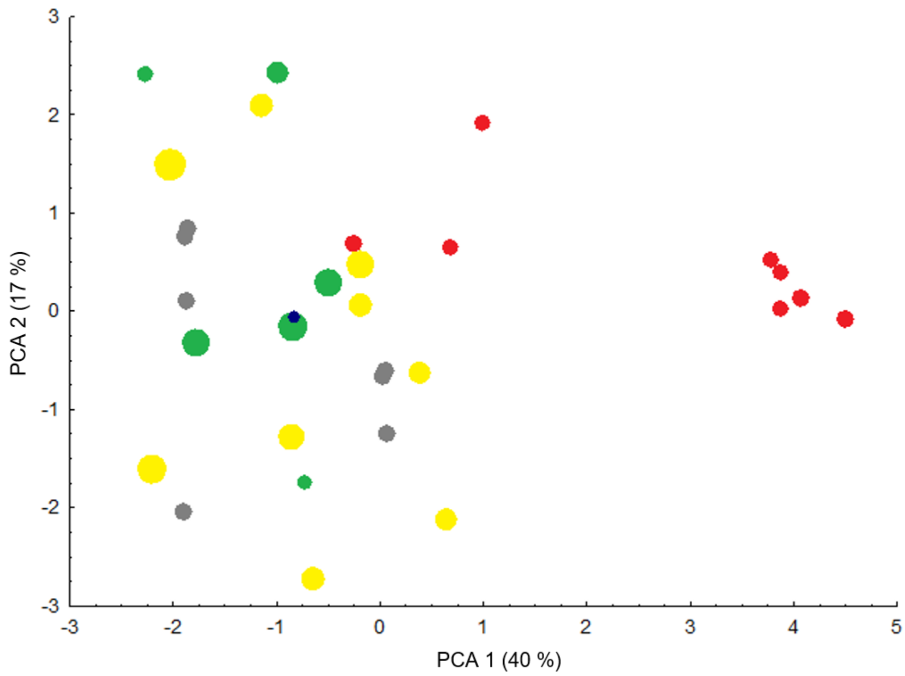

Figure 6. Ordination of reference streams based on the variation of most relevant channel morphology characteristics. Mean elevation of stream reaches is directly proportional to the diameter of the circles. The color of the circles indicates the National Park in which reaches are located: blue = Cavernas do Peruaçu National Park; green = Sempre-Vivas National Park; grey = Serra do Cipó National Park; red= Grande Sertão Veredas National Park; yellow = Serra da Canastra National Park.

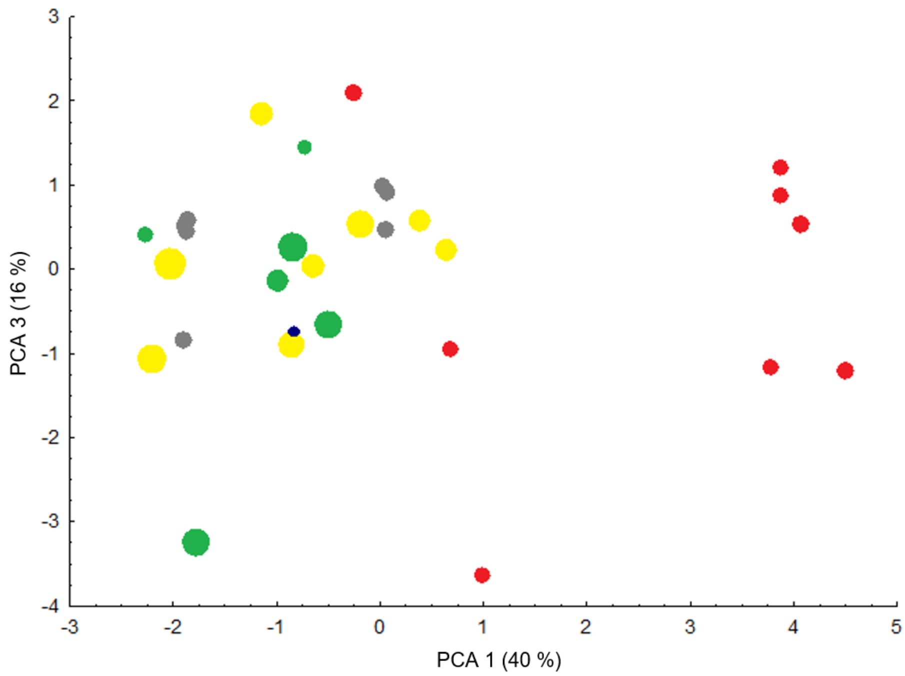

Figure 7. Ordination of reference streams based on the variation of most relevant channel morphology characteristics related. Mean elevation of stream reaches is directly proportional to the diameter of the circles. The color of the circles indicates the National Park in which reaches are located: blue = Cavernas do Peruaçu National Park; green = Sempre-Vivas National Park; grey = Serra do Cipó National Park; red= Grande Sertão Veredas National Park; yellow = Serra da Canastra National Park.

Geographic position explained part of the variation of channel morphology characteristics as suggested by the PCA plot for the streams (Table 1). Water flow also explained part of the variation in channel morphology charcateristics. The variables 'geographic position' and 'water flow' respectively explained 27 and 9% of variation in channel morphology among streams when considered by themselves. Moreover, the best statistically significant model (adjusted R^2 = 0.26; $P = 0.03$) included 'geographic position' and 'water flow' as predictor variables. In the model, 'geographic position' explained 22% of the variation (Table 1) and 'water flow' added 4% of explanation power to it. 'Mean elevation' did not contribute to the explanation of the variation of channel morphology characteristics which contradicted our expectations from the PCA plot.

Discussion

Physical habitat standards for reference streams should be set at a local rather than a regional or hydrographic basin scale, and preferably for streams with similar elevation and water flow. Streams along the São Francisco river basin in Minas Gerais presented a large variation of physical habitat conditions. Percentage of fine sediment on the streambed, percentage of dissolved oxygen in water, and mean percentage canopy cover over the stream channel were some of the characteristics that presented a wide range of values among reference streams. That variation of stream characteristics was partially explained by the geographic position of streams and secondarily by mean elevation or water flow of streams once geographic position of streams was already taken into account. Hence, precise comparisons of streams based on the reference condition approach should first seek to establish a regional scale at which macro environmental conditions are homogenous. Then, one should separate regional streams into categories based on ranges of elevation and mean water flow, and compare streams which belong to the same categories.

Geographic position explained part of the variation of all five categories of physical habitat characteristics of reference streams (water chemistry, substrate, fish shelter, riparian vegetation, and channel morphology). The importance of geographic position for physical habitat characteristics of streams reflects geological, geomorphological, and climatic variations in the landscape (Montgomery 1999). Reference streams naturally presented a wide range of values for water chemistry metrics. Water chemistry characteristics (e.g. dissolved oxygen concentration) often are used as proxy for water quality and habitat alteration assessment (Wiegner *et al*. 2013; Potter *et al*. 2014; Amuchástegui *et al*. 2016). Unfortunately, water chemistry natural variations among freshwater ecosystems are commonly neglected. In this study, the variation of water temperature and dissolved oxygen concentration among reference streams were partially explained by the geographic position of reaches probably because they are directly affected by air temperature of the region and canopy cover (Hetrick *et al*. 1998; Caissie *et al*. 2001). Water flow characteristics of streams (e.g. turbulence) are also influenced by water temperature and concentration of dissolved oxygen (Demars & Manson 2013). In addition, local temperature, precipitation, lithology, organic matter input, and water flow may also influence local rates of erosion and decomposition (García-Ruiz *et al*. 2015). Thus, minerals from substrate erosion and organic compounds from decomposition may have contributed for the natural differences in pH and conductivity among reference streams.

The differences between substrates of stream reaches in PARNA Grande Sertão Veredas and stream reaches in PARNA Serra da Canastra, PARNA Serra do Cipó, and PARNA Sempre-Vivas was possibly related to differences in predominant geological formations in the region of each park. Large fine sediment deposits in streams are commonly associated with human impacts such as riparian vegetation removal (Chutter 1969; Harding & Winterbourn 1995). But the abundance of fine sediments on the streambeds in PARNA Grande Sertão Veredas is a natural consequence of the predominance of arenites and siltstones in the region, which are easily erodible geological formations (IBAMA & FUNATURA 2003; Fragoso *et al*. 2011). On the other hand, PARNA Serra da Canastra is geologically located in the Canastra Group while PARNA Serra do Cipó e PARNA Sempre-Vivas are located in the Espinhaço Supergroup. Both lithologies are mainly formed by quartzite (Pereira *et al*. 1994; Saadi 1995) which is more difficultly eroded than arenite and sandstone. Therefore, mean substrate size on streambeds was naturally bigger in PARNA Serra da Canastra, PARNA Serra do Cipó, and PARNA Sempre-Vivas than in PARNA Grande Sertão Veredas.

Part of the variation in mean sediment size of reaches may also be attributed to natural elevation dependent hydraulics. Local lithology and human land use often are common explanations proposed for differences in sediment dimension (Harding & Winterbourn 1995; García-Ruiz *et al*. 2015). In this study, those explanations did not apply because stream reaches in a same region ran over the same general lithology and were all located inside protected areas with little human interference. Besides regional aspects such as lithology and hydrology, substrate profiles of reference streams may also be naturally influenced by local environmental aspects. For instance, hydraulic features associated with mean elevation of stream reaches may partially explain the decrease in average sediment size with decreasing elevation (Asfaha *et al*. 2015). Bedrock and boulders were common in high elevation reaches but were gradually substituted by cobble, sand and fine sediments as elevation decreased. Streams usually have greater slope and less suspended sediment at high elevation and that allows them to remove smaller sediment and leave only coarse sediment on the streambed of reaches with high mean elevation (Hubert & Kozel 1993; Lipsey *et al*. 2005). As elevation decreases, the slope of streams usually decreases and the amount of suspended sediment increases, which reduces the energy available for water to erode the substrate and move fine sediment downstream. Hence, increasingly smaller sediments are deposited on the streambed as mean elevation of reaches decreases and that may explain part of the natural variation observed for the substrate profile of reference stream.

Geographic position and mean elevation of stream reaches explained almost the same amount of the observed variance for fish shelter profile and riparian vegetation structure of reference streams. The riparian vegetation of tropical streams is often depicted as a dense gallery forest with a plethora woody plant species. Even though that is an accurate description in many cases, some tropical streams may naturally have only grasses and shrubs for their riparian vegetation (Teresa & Romero 2010). Thus, variance in vegetation-related fish shelter profile and riparian vegetation structure among reference streams may partially be explained by differences in local phytophysiognomies. The regional pool of plant species and local environmental conditions influence the structure of the riparian vegetation of streams which is directly associated with instream fish shelter profile and abundance (Hrodey & Sutton 2008; Teresa *et al*. 2015). Riparian vegetation in grasslands will have mostly grasses and low shrubs which will provide little canopy cover and few wood debris for fish shelter but will allow high densities of algae and macrophytes (Ribeiro *et al*. 1998; Riley & Dodds 2012; Oliveira *et al*. 2013). Gallery forests and ‘veredas’ will work in the opposite way as grasslands because of the presence of many tall trees and woody plants in their riparian vegetation. Stream reaches in PARNA Grande Sertão Veredas were mainly low elevation ‘veredas’ stream reaches which had dense canopy cover, high densities of roots, high input of wood debris and leaf litter, and low densities of algae and macrophytes. The stream reach sampled in PARNA Cavernas do Peruaçu was located in a low elevation wet portion of the park and it had a well-developed gallery forest for its riparian vegetation. Its riparian vegetation structure was similar to those from PARNA Grande Sertão Veredas although the plant species composition was different. Plant roots were the main component of its fish shelter profile. In contrast, PARNA Serra da Canastra, PARNA Serra do Cipó, and PARNA Sempre-Vivas are located in mountainous regions where there was predominance of grasslands at high elevations and grasslands with gallery forests along streams at low elevations (Ribeiro *et al*. 1998). Hence, canopy cover and fish shelter of streams provided by woody plants decreased as mean reach elevation of streams increased in those regions. Thus, environmental conditions of stream reaches determined by geographic position and mean elevation of reaches may explain important natural differences among riparian vegetation structure and fish shelter profile of reference streams.

Streams in PARNA Grande Sertão Veredas naturally had the highest mean water velocity and percentage of fast-flowing sections although they had the second lowest average streambed slope. In streams, fast-flowing water usually is associated to high streambed slope and coarse substrate (Hubert & Kozel 1993) and associations different from that one often are attributed to human impacts on lotic systems (Ritcher *et al*. 1997). Thus, stream reaches in PARNA Grande Sertão Veredas had a peculiar natural combination of channel morphology characteristics. The geographic position of those streams partially explained that combination. PARNA Grande Sertão Veredas is located in a very humid depression among xeric highlands of the Cerrado and it has many wetlands ecosystems known as 'veredas'. Veredas' streams have large water flows throughout the entire year despite being low order streams because rainfall easily infiltrates in the region's sandy soil and recharges the water tables. Since water tables are shallow in 'veredas', streams have a constant source of water and large water flow even during the dry season in those ecosystems (Ferreira 2008). On the other hand, PARNA Serra da Canastra, PARNA Serra do Cipó, and PARNA Sempre-Vivas have typical tropical second and third order mountainous streams with great seasonal variation of the water flow (Covich *et al*. 2003). Therefore, a lower number of fast-flowing sections may be associated with natural low water flow during the dry season. Additionally, large substrate (e.g. boulders) can help create slow-flowing conditions acting as flow-barriers when water level is low in those streams (Wohl & Legleiter 2003; Yarnell *et al*. 2006). PARNA Cavernas do Peruaçu is different from the other parks because it is located in a very dry region and its groundwater is very deep due to the karstic soil in the region (Bailly-Comte *et al*. 2009). Those regional conditions help explain the low water flow and the predominance of slow-flowing transects in the sampled stream. Those same conditions may also be the reason why the park had only one perennial surface stream that could be sampled during the dry season.

Here, it was presented a thorough analysis of the natural variations of physical habitat conditions among reference streams and some of their possible drivers. Knowledge on the natural variation of physical habitat conditions of reference streams is an important step toward the conservation of tropical streams because freshwater beta diversity is directly influenced by regional habitat heterogeneity (Campbell *et al*. 2012; Heino *et al*. 2015). Thus, the relationship between geographic position, mean elevation, and water flow and the natural variation of physical habitat conditions of streams that we attested in this study is a relevant contribution to freshwater conservation. Nevertheless, the chosen explanatory variables did not explain the entire measured variation. It is true that such large natural variation must be influenced by a myriad of factors and that it is impossible to account for all of them. Still, it is possible that regional land use analysis and temporal variation may elucidate part of the unexplained variation of physical habitat characteristics among reference streams. Hence, temporal replicates of the sampled reaches could increase the explanation power of the adopted explanatory variables (Grove *et al*. 2015). The sampling period was drier than the usual for the season and that may have interfered with measured values, especially those of flow-dependent metrics. Thus, resampling the streams one or more times could indicate a stronger relation between explanatory and resulting variables. Furthermore, reference streams could have been indirectly affected by runoffs and water table contaminants from impacted areas adjacent to the parks despite them being protected from most human interference (Allan 2004; Gordon et al. 2008). Nevertheless, those impacts were minimum for the sampled streams because all of them had their entire extension and drainage basin inside the protected areas.

This study is the broadest and most detailed description of the physical habitat conditions of reference streams in a Brazilian river basin so far, and its results support a local-scale framework for future studies involving tropical reference streams. The “reference condition” is still a generally neglected theme in tropical research despite its great importance and applicability in environmental impact and alteration assessment. Additionally, this field of research may generate valuable information on the status of threatened but yet understudied systems such as most Neotropical low-order streams ecosystems. Hence, the development of this research field in the tropical region could be a major contribution to science and environmental conservation.

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Supplementary Table 1 (S1). Values for reference streams' physical-habitat metrics in five national parks (PARNA) in the São Francisco river basin, Brazil. Parks were identified as follows: **CA** - PARNA Serra da Canastra; **CI** - PARNA Serra do Cipó; **CP** - PARNA Cavernas do Peruaçu; **SV** - PARNA Sempre-Vivas; **GS** - PARNA Grande Sertão Veredas. Standard deviation and missing values are represented by 'SD' and 'NA', respectively.

Metrics	**CA**		**CI**		**CP**		**SV**		**GS**	
	Mean	**(Min / Max)**	**Mean**	**(Min / Max)**	**Mean**	**(Min / Max)**	**Mean**	**(Min / Max)**	**Mean**	**(Min / Max)**
Water chemistry										
Temperature (°C)	18.94	(10.59 / 22.54)	20.30	(18.00 / 24.21)	19.11	(19.11 / 19.11)	20.32	(17.09 / 22.29)	21.16	(19.67 / 22.14)
pH	5.68	(4.85 / 6.73)	NA	(NA / NA)	7.31	(7.31 / 7.31)	7.01	(6.39 / 7.55)	7.73	(7.11 / 7.92)
Conductivity 1 (µS/cm)	7.55	(2.40 / 14.6)	6.73	(2.22 / 17.93)	1038.00	(1038.00 / 1038.00)	0.62	(0.19 / 1.33)	0.21	(0.092 / 0.384)
Conductivity 2 (µS/cm)	6.88	(2.20 / 13.70)	4.16	(0 / 11.3)	921.00	(921.00 / 921.00)	467.63	(3.78 / 1251)	0.19	(0.084 / 0.359)
Dissolved oxygen (mg/L)	15.86	(5.13 / 86.00)	7.95	(6.94 / 8.46)	6.97	(6.97 / 6.97)	18.82	(5.39 / 78)	6.24	(4.85 / 7.86)
Dissolved oxygen (%)	72.26	(7.70 / 91.60)	88.61	(78 / 97.8)	75.60	(75.60 / 75.60)	66.65	(7.48 / 93.2)	69.78	(54.20 / 90.30)
Substrate										
Channel's and margins' substrate average immersion (%)	32.03	(23.82 / 41.63)	36.26	(14.73 / 70.36)	58.82	(58.82 / 58.82)	28.71	(3.64 / 42.09)	74.03	(11.67 / 95.09)
SD of channel's and margins' substrate average immersion (%)	29.78	(22.15 / 34.20)	28.43	(18.91 / 39.91)	44.14	(44.14 / 44.14)	35.15	(14.45 / 46.91)	26.86	(13.44 / 49.03)
channel's substrate average immersion (%)	31.13	(24.85 / 45.76)	35.89	(15.15 / 69.39)	56.06	(56.06 / 56.06)	26.19	(2.12 / 39.85)	76.91	(10.15 / 100.00)

SD of channel's substrate average immersion (%)	27.33	(18.36 / 33.34)	28.26	(19.19 / 40.31)	45.08	(45.08 / 45.08)	32.23	(6.50 / 45.98)	23.13	(0.00 / 50.75)
Smooth bedrock (%)	11.85	(0.00 / 38.10)	6.80	(0.00 / 27.62)	0.00	(0.00 / 0.00)	5.44	(0.00 / 21.90)	0.12	(0.00 / 0.97)
Rugged bedrock (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	2.93	(0.00 / 7.77)	0.97	(0.00 / 7.77)
Bedrock (smooth + rugged) (%)	11.85	(0.00 / 38.10)	6.80	(0.00 / 27.62)	0.00	(0.00 / 0.00)	8.37	(2.86 / 22.86)	1.09	(0.00 / 8.74)
Large boulder (%)	5.50	(0.00 / 11.43)	13.71	(0.00 / 47.62)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	2.74	(0.00 / 17.14)
Small boulder (%)	24.34	(0.00 / 40.00)	26.85	(0.00 / 47.00)	0.00	(0.00 / 0.00)	7.85	(0.00 / 14.29)	0.00	(0.00 / 0.00)
Boulder (large + small) (%)	29.84	(0.00 / 51.43)	40.56	(0.00 / 71.43)	0.00	(0.00 / 0.00)	7.85	(0.00 / 14.29)	2.74	(0.00 / 17.14)
Cobble (%)	18.24	(5.71 / 39.05)	15.03	(0.00 / 33.33)	13.33	(13.33 / 13.33)	4.04	(0.00 / 20.39)	3.40	(0.00 / 27.18)
Coarse gravel (%)	9.44	(2.86 / 21.15)	9.44	(1.90 / 20.00)	0.95	(0.95 / 0.95)	4.22	(0.00 / 16.50)	0.97	(0.00 / 7.77)
Substrate > 16 mm diameter (%)	69.37	(47.62 / 89.52)	71.84	(3.00 / 97.00)	14.29	(14.29 / 14.29)	24.47	(7.29 / 41.75)	8.20	(0.00 / 43.69)
Fine gravel (%)	10.40	(0.95 / 25.00)	9.66	(0.00 / 20.00)	5.71	(5.71 / 5.71)	0.00	(0.00 / 0.00)	0.36	(0.00 / 2.91)
Sand (%)	5.40	(0 / 15.24)	10.31	(0.00 / 56.00)	1.90	(1.90 / 1.90)	10.57	(0.00 / 25.00)	4.84	(0.00 / 33.01)
Fine (%)	1.17	(0.00 / 5.77)	1.27	(0.00 / 7.00)	46.67	(46.67 / 46.67)	4.85	(0.00 / 24.27)	23.34	(0.00 / 92.38)
Substrate < 16 mm diameter (%)	16.96	(2.86 / 30.77)	21.24	(0.00 / 83.00)	54.29	(54.29 / 54.29)	15.43	(1.90 / 26.04)	28.55	(0.00 / 92.38)
Total organic (%)	10.49	(2.86 / 32.38)	6.78	(0.00 / 14.00)	5.71	(5.71 / 5.71)	117.12	(100.95 / 131.25)	54.92	(0.95 / 97.14)

Wood (%)	0.00	(0.00 / 0.00)	0.85	(0.00 / 5.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	1.94	(0.00 / 15.53)
Concrete (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	2.93	(0.00 / 7.77)	0.97	(0.00 / 7.77)
Hard pan (%)	0.85	(0.00 / 5.77)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.83	(0.00 / 6.67)
Other (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.95	(0.00 / 4.76)	0.00	(0.00 / 0.00)
Roots (%)	2.12	(0.00 / 7.62)	1.50	(0.00 / 4.76)	0.00	(0.00 / 0.00)	0.32	(0.00 / 1.94)	45.36	(0.00 / 87.62)
Fine litter (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	100.00	(100.00 / 100.00)	3.93	(0.00 / 10.48)
Coarse litter (%)	8.16	(0.00 / 28.57)	3.75	(0.00 / 8.00)	5.71	(5.71 / 5.71)	11.10	(0.95 / 28.13)	3.69	(0.00 / 16.19)
Filamentous algae (%)	0.21	(0.00 / 1.90)	0.68	(0.00 / 3.81)	0.00	(0.00 / 0.00)	5.70	(0.00 / 18.45)	0.00	(0.00 / 0.00)
Aquatic macrophyte (%)	0.74	(0.00 / 3.81)	0.14	(0.00 / 0.95)	0.95	(0.95 / 0.95)	23.33	(0.00 / 62.86)	0.12	(0.00 / 0.95)
Small sediment on channel bed (%)	0.08	(0.00 / 0.24)	0.11	(0.00 / 0.67)	0.67	(0.67 / 0.67)	0.10	(0.00 / 0.21)	0.84	(0.06 / 1.00)
Mean substrate size	0.25	(0.16 / 0.30)	0.20	(-0.03 / 0.29)	-0.11	(-0.11 / -0.11)	0.25	(0.07 / 0.39)	-0.07	(-0.26 / 0.24)
Filamentous algae + aquatic macrophyte (%)	0.95	(0.00 / 4.76)	0.82	(0.00 / 4.76)	0.95	(0.95 / 0.95)	29.03	(3.13 / 62.86)	0.12	(0.00 / 0.95)
Roots + fine litter + coarse litter (%)	10.27	(2.86 / 32.38)	5.25	(0.00 / 11.43)	5.71	(5.71 / 5.71)	111.42	(100.95 / 128.13)	52.98	(0.00 / 97.14)
Sand + fine (%)	6.57	(0.00 / 15.24)	11.59	(0.00 / 63.00)	48.57	(48.57 / 48.57)	15.43	(1.90 / 26.04)	28.19	(0.00 / 92.38)
Log10 [estimated geometric mean substrate diameter (mm)]	2.04	(1.19 / 2.57)	2.00	(-0.24 / 2.73)	-0.69	(-0.69 / -0.69)	-22.06	(-109.54 / -0.29)	-0.48	(-1.91 / 0.93)

Log10 [relative bed stability]	1.31	(-0.43 / 2.81)	1.57	(-1.58 / 2.69)	-0.93	(-0.93 / -0.93)	-22.34	(-109.30 / -0.67)	-0.82	(-2.75 / 0.68)
Relative bed stability	0.72	(-0.39 / 1.61)	0.43	(-0.21 / 1.34)	0.24	(0.24 / 0.24)	0.28	(-0.23 / 0.71)	0.35	(-0.28 / 0.85)
Deviation of substrate diameter	0.40	(0.26 / 0.54)	0.35	(0.14 / 0.53)	0.55	(0.55 / 0.55)	0.58	(0.31 / 0.98)	0.33	(0.15 / 0.75)
Fish shelter										
Filamentous algae areal cover	1.19	(0.00 / 8.41)	37.37	(0.00 / 84.77)	0.00	(0.00 / 0.00)	9.09	(0.00 / 33.41)	0.00	(0.00 / 0.00)
Aquatic macrophyte areal cover	8.84	(0.00 / 39.55)	10.65	(0.00 / 42.95)	0.00	(0.00 / 0.00)	22.65	(0.00 / 55.91)	5.82	(0.00 / 25.91)
Large woody debris areal cover	1.39	(0.00 / 10.23)	1.56	(0.00 / 9.55)	0.00	(0.00 / 0.00)	0.45	(0.00 / 1.82)	2.78	(0.00 / 5.45)
Brush and small woody debris areal cover	22.98	(0.00 / 57.05)	7.31	(0.00 / 26.82)	23.18	(23.18 / 23.18)	5.15	(1.82 / 19.09)	46.79	(0.00 / 87.50)
Root areal cover	6.74	(0.00 / 17.73)	22.60	(5.68 / 70.91)	43.86	(43.86 / 43.86)	11.17	(4.55 / 23.41)	37.27	(0.00 / 84.77)
Leaf bank areal cover	54.32	(0.45 / 87.50)	35.26	(0.00 / 82.05)	22.95	(22.95 / 22.95)	25.19	(0.00 / 71.14)	37.64	(0.00 / 84.77)
Overhanging vegetation areal cover	11.64	(0.45 / 34.77)	16.79	(5.45 / 48.64)	21.59	(21.59 / 21.59)	26.82	(1.36 / 57.27)	32.98	(6.82 / 87.50)
Undercut bank areal cover	9.04	(0.00 / 25.00)	16.95	(0.00 / 40.00)	0.00	(0.00 / 0.00)	2.42	(0.00 / 5.45)	8.27	(0.00 / 41.82)
Boulder areal cover	67.98	(3.64 / 87.50)	66.53	(0.00 / 87.50)	0.91	(0.91 / 0.91)	48.33	(4.55 / 87.50)	11.22	(0.00 / 87.50)
Artificial structure areal cover	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Total areal cover for fish except filamentous algae and aquatic macrophytes	174.09	(96.82 / 250.23)	166.98	(105.91 / 288.64)	112.50	(112.50 / 112.50)	119.55	(41.82 / 188.64)	176.96	(80.00 / 370.23)

Total areal cover for fish	184.12	(107.50 / 250.23)	215.00	(133.18 / 352.50)	112.50	(112.50 / 112.50)	151.29	(107.05 / 200.68)	182.78	(80.00 / 370.23)
Total areal cover of large wood, brush, overhanging vegetation, boulders, and undercut banks	113.03	(90.23 / 145.45)	109.12	(72.05 / 140.91)	45.68	(45.68 / 45.68)	83.18	(30.68 / 141.14)	102.05	(53.64 / 220.00)
Total areal cover of large wood, brush, overhanging vegetation, boulders, undercut banks, leaf banks, and roots	174.09	(96.82 / 250.23)	166.98	(105.91 / 288.64)	112.50	(112.50 / 112.50)	119.55	(41.82 / 188.64)	176.96	(80.00 / 370.23)
Anthropogenic structures areal cover	10.03	(0.00 / 47.95)	48.02	(0.00 / 127.73)	0.00	(0.00 / 0.00)	31.74	(0.00 / 89.32)	5.82	(0.00 / 25.91)
Total areal cover of large wood, boulders, undercut banks, and human structures	78.41	(19.55 / 100.45)	85.03	(39.77 / 100.68)	0.91	(0.91 / 0.91)	51.21	(5.91 / 89.32)	22.27	(0.00 / 88.41)
Filamentous algae and aquatic macrophyte areal cover	10.03	(0.00 / 47.95)	48.02	(0.00 / 127.73)	0.00	(0.00 / 0.00)	31.74	(0.00 / 89.32)	5.82	(0.00 / 25.91)
Large and small woody debris areal cover	24.37	(0.00 / 57.05)	8.86	(0.00 / 36.36)	23.18	(23.18 / 23.18)	5.61	(1.82 / 20.91)	49.57	(0.00 / 90.68)
Roots and overhanging vegetation areal cover	18.38	(0.91 / 45.23)	39.38	(13.18 / 89.32)	65.45	(65.45 / 65.45)	37.99	(5.91 / 75.45)	70.26	(12.50 / 172.27)
Proportion of reach with filamentous algae cover	0.03	(0.00 / 0.18)	0.77	(0.00 / 1.00)	0.00	(0.00 / 0.00)	0.33	(0.00 / 0.91)	0.00	(0.00 / 0.00)
Proportion of reach with aquatic macrophyte cover	0.17	(0.00 / 0.55)	0.29	(0.00 / 0.73)	0.00	(0.00 / 0.00)	0.79	(0.00 / 1.00)	0.18	(0.00 / 0.91)
Proportion of reach with large woody debris cover	0.09	(0.00 / 0.36)	0.16	(0.00 / 0.82)	0.00	(0.00 / 0.00)	0.09	(0.00 / 0.36)	0.28	(0.00 / 0.55)
Proportion of reach with small woody debris cover	0.54	(0.00 / 1.00)	0.36	(0.00 / 0.91)	0.91	(0.91 / 0.91)	0.44	(0.36 / 0.64)	0.81	(0.00 / 1.00)
Proportion of reach with root cover	0.24	(0.00 / 0.55)	0.55	(0.18 / 1.00)	1.00	(1.00 / 1.00)	0.71	(0.36 / 1.00)	0.63	(0.00 / 1.00)
Proportion of reach with leaf bank cover	0.87	(0.09 / 1.00)	0.77	(0.00 / 1.00)	1.00	(1.00 / 1.00)	0.56	(0.00 / 1.00)	0.74	(0.00 / 1.00)
Proportion of reach with overhanging vegetation cover	0.44	(0.09 / 0.91)	0.69	(0.18 / 0.91)	0.91	(0.91 / 0.91)	0.83	(0.27 / 1.00)	0.91	(0.64 / 1.00)

Proportion of reach with undercut bank cover	0.35	(0.00 / 0.91)	0.44	(0.00 / 1.00)	0.00	(0.00 / 0.00)	0.24	(0.00 / 0.55)	0.30	(0.00 / 1.00)
Proportion of reach with boulder cover	0.92	(0.36 / 1.00)	0.79	(0.00 / 1.00)	0.18	(0.18 / 0.18)	0.85	(0.55 / 1.00)	0.14	(0.00 / 1.00)
Proportion of reach with artificial structure cover	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Proportion of reach with any cover except filamentous algae and aquatic macrophyte	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with any cover	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with large wood, brush, overhanging vegetation, boulders, or undercut banks cover	1.00	(1.00 / 1.00)	0.99	(0.91 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with large wood, brush, overhanging vegetation, boulders, undercut banks, leaf banks, or roots cover	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with anthropogenic structures	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with large wood, boulders, undercut banks, or human structures cover	0.18	(0.00 / 0.64)	0.81	(0.00 / 1.00)	0.00	(0.00 / 0.00)	0.79	(0.00 / 1.00)	0.18	(0.00 / 0.91)
Riparian vegetation										
Mean canopy density mid-stream (%)	71.51	(12.43 / 99.87)	60.39	(17.11 / 99.73)	94.79	(94.79 / 94.79)	38.86	(5.88 / 83.42)	82.62	(37.30 / 100.00)
SD of mean canopy density mid-stream (%)	16.65	(0.44 / 36.83)	24.17	(0.59 / 42.31)	2.66	(2.66 / 2.66)	28.39	(15.35 / 40.63)	8.15	(0.00 / 24.65)
Mean canopy density at bank (%)	80.60	(24.33 / 99.47)	76.32	(51.34 / 99.73)	97.33	(97.33 / 97.33)	52.99	(22.19 / 91.98)	91.34	(50.80 / 100.00)
SD of mean canopy density at bank (%)	13.91	(1.77 / 35.45)	21.57	(0.89 / 40.32)	3.34	(3.34 / 3.34)	26.54	(9.12 / 37.06)	7.45	(0.00 / 26.38)

Riparian canopy (> 5 m high) cover - trees > 0.3 m DBH	3.61	(0.00 / 6.82)	3.15	(0.23 / 12.05)	5.00	(5.00 / 5.00)	1.89	(0.23 / 4.55)	4.35	(0.68 / 11.02)
SD of riparian canopy (> 5 m high) cover - trees > 0.3 m DBH	4.43	(0.00 / 9.26)	3.17	(0.75 / 5.93)	6.02	(6.02 / 6.02)	2.31	(0.75 / 4.40)	6.19	(1.17 / 16.80)
Riparian canopy (> 5 m high) cover - trees < 0.3 m DBH	26.70	(0.00 / 63.86)	14.81	(4.55 / 40.80)	22.39	(22.39 / 22.39)	16.21	(1.82 / 36.82)	47.22	(9.77 / 84.77)
SD of riparian canopy (> 5 m high) cover - trees < 0.3 m DBH	14.56	(0.00 / 20.43)	14.37	(5.90 / 34.75)	13.21	(13.21 / 13.21)	10.45	(1.17 / 17.30)	18.39	(9.05 / 37.44)
Riparian mid-layer (0.5 to 5 m high) woody cover	15.49	(3.75 / 31.14)	13.96	(2.50 / 25.23)	55.68	(55.68 / 55.68)	24.47	(4.09 / 41.70)	20.63	(0.00 / 60.80)
SD of riparian mid-layer (0.5 to 5 m high) woody cover	17.03	(9.10 / 24.11)	10.96	(5.00 / 18.08)	25.43	(25.43 / 25.43)	12.03	(6.88 / 20.99)	15.53	(0.00 / 29.96)
Riparian mid-layer (0.5 to 5 m high) herbaceous cover	9.85	(0.00 / 27.16)	12.53	(5.23 / 27.95)	20.23	(20.23 / 20.23)	6.06	(0.45 / 10.91)	49.90	(0.00 / 87.50)
SD of riparian mid-layer (0.5 to 5 m high) herbaceous cover	12.95	(0.00 / 29.72)	12.08	(5.03 / 17.66)	21.28	(21.28 / 21.28)	4.67	(1.01 / 10.37)	19.85	(0.00 / 37.26)
Riparian ground-layer (< 0.5 m high) woody cover	7.13	(0.23 / 39.55)	28.18	(18.52 / 41.70)	9.55	(9.55 / 9.55)	7.22	(0.00 / 13.30)	13.59	(1.36 / 40.91)
SD of riparian ground-layer (< 0.5 m high) woody cover	8.41	(0.75 / 29.31)	21.51	(13.53 / 30.90)	19.73	(19.73 / 19.73)	6.62	(0.00 / 12.02)	16.79	(4.52 / 38.15)
Riparian ground-layer (< 0.5 m high) herbaceous cover	39.63	(2.61 / 65.11)	33.96	(17.84 / 56.02)	25.45	(25.45 / 25.45)	27.48	(4.09 / 58.98)	46.45	(21.93 / 87.50)
SD of riparian ground-layer (< 0.5 m high) herbaceous cover	23.15	(8.67 / 32.78)	19.42	(11.47 / 27.23)	25.21	(25.21 / 25.21)	15.08	(5.51 / 29.93)	16.94	(0.00 / 30.76)
Riparian ground-layer (< 0.5 m high) bare ground cover	26.41	(0.00 / 79.55)	15.89	(0.23 / 43.52)	0.00	(0.00 / 0.00)	35.23	(11.36 / 56.02)	10.65	(0.00 / 52.27)
SD of riparian ground-layer (< 0.5 m high) bare ground cover	15.56	(0.00 / 32.19)	14.27	(0.75 / 25.28)	0.00	(0.00 / 0.00)	19.30	(10.73 / 31.42)	5.00	(0.00 / 21.00)
Riparian canopy cover (XCL + XCS)	30.32	(0.00 / 70.57)	17.95	(4.77 / 45.11)	27.39	(27.39 / 27.39)	18.11	(2.05 / 41.36)	51.56	(20.80 / 87.84)

SD of riparian canopy cover (XCL + XCS)	15.68	(0.00 / 22.36)	16.02	(6.27 / 38.94)	17.07	(17.07 / 17.07)	10.70	(1.51 / 17.43)	19.02	(8.59 / 37.57)
Riparian mid-layer cover (XMW + XMH)	25.34	(7.05 / 51.14)	26.49	(10.23 / 49.43)	75.91	(75.91 / 75.91)	30.53	(4.77 / 49.20)	70.53	(22.95 / 148.30)
SD of riparian mid-layer cover (XMW + XMH)	21.21	(10.79 / 37.54)	17.86	(8.70 / 30.07)	30.12	(30.12 / 30.12)	12.97	(7.94 / 22.97)	28.16	(20.17 / 37.85)
Riparian ground-layer vegetation cover (XGW + XGH)	46.77	(3.75 / 101.48)	62.14	(36.36 / 97.73)	35.00	(35.00 / 35.00)	34.70	(4.09 / 65.80)	60.04	(23.30 / 124.32)
SD odf riparian ground-layer vegetation cover (XGW + XGH)	26.25	(9.10 / 38.86)	34.88	(22.09 / 52.41)	31.63	(31.63 / 31.63)	16.88	(5.51 / 25.44)	26.74	(16.86 / 41.41)
Riparian canopy + mid-layer cover (XC + XM)	55.66	(17.16 / 83.75)	44.45	(15.00 / 65.68)	103.30	(103.30 / 103.30)	48.64	(22.61 / 79.20)	122.09	(43.75 / 196.36)
SD of riparian canopy + mid-layer cover (XC + XM)	26.24	(15.05 / 50.37)	26.42	(13.70 / 48.90)	32.09	(32.09 / 32.09)	18.28	(8.44 / 28.49)	35.20	(24.71 / 52.30)
Riparian canopy + mid-layer woody cover (XC + XM)	45.81	(9.55 / 78.30)	31.92	(7.27 / 50.80)	83.07	(83.07 / 83.07)	42.58	(21.93 / 68.30)	72.19	(33.07 / 120.91)
SD of riparian canopy + mid-layer woody cover (XC + XM)	23.01	(15.05 / 37.51)	20.55	(6.66 / 37.93)	23.13	(23.13 / 23.13)	17.27	(7.25 / 27.35)	21.74	(8.59 / 35.23)
Riparian cover, sum of 3 layers (XC + XM + XG)	102.42	(78.41 / 124.20)	106.59	(76.36 / 163.41)	138.30	(138.30 / 138.30)	83.33	(26.70 / 124.77)	182.13	(121.82 / 320.68)
SD of riparian cover, sum of 3 layers (XC + XM + XG)	28.00	(15.17 / 45.00)	33.99	(22.91 / 44.96)	33.82	(33.82 / 33.82)	25.07	(12.65 / 37.67)	32.10	(19.70 / 50.52)
Riparian woody cover, sum of 3 layers (XC + XMW + XGW)	52.94	(25.68 / 79.43)	60.10	(37.50 / 79.66)	92.61	(92.61 / 92.61)	49.79	(21.93 / 81.14)	85.78	(40.11 / 149.77)
SD of riparian woody cover, sum of 3 layers (XC + XMW + XGW)	24.28	(12.23 / 34.50)	24.76	(14.65 / 41.83)	34.85	(34.85 / 34.85)	18.86	(8.02 / 29.82)	22.24	(4.16 / 35.03)
Riparian canopy presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Riparian mid-layer presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)

Riparian ground cover presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Riparian canopy and mid-layer presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
3-layer riparian vegetation presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Large wood debris in active channel (pieces/100 m) - size class 1	4.89	(0.00 / 17.33)	8.86	(0.00 / 50.67)	17.33	(17.33 / 17.33)	1.00	(0.00 / 4.00)	16.33	(0.67 / 30.67)
Large wood debris in active channel (pieces/100 m) - size class 2	1.11	(0.00 / 5.33)	1.81	(0.00 / 10.00)	1.33	(1.33 / 1.33)	0.00	(0.00 / 0.00)	3.58	(0.00 / 10.67)
Large wood debris in active channel (pieces/100 m) - size class 3	0.00	(0.00 / 0.00)	0.67	(0.00 / 3.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.17	(0.00 / 0.67)
Large wood debris in active channel (pieces/100 m) - size class 4	0.00	(0.00 / 0.00)	0.19	(0.00 / 1.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/100 m) - size class 1	0.63	(0.00 / 2.87)	2.38	(0.00 / 14.41)	1.37	(1.37 / 1.37)	0.06	(0.00 / 0.23)	2.19	(0.04 / 5.18)
Large wood debris volume in active channel (m^3/100 m) - size class 2	0.00	(0.00 / 0.00)	1.63	(0.00 / 10.03)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.17	(0.00 / 0.69)
Large wood debris volume in active channel (m^3/100 m) - size class 3	0.41	(0.00 / 2.18)	1.97	(0.00 / 12.05)	0.44	(0.44 / 0.44)	0.00	(0.00 / 0.00)	1.45	(0.00 / 4.02)
Large wood debris volume in active channel (m^3/100 m) - size class 4	0.00	(0.00 / 0.00)	1.14	(0.00 / 7.95)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/100 m) - size class 1	2.30	(0.00 / 8.67)	5.81	(0.00 / 32.00)	6.67	(6.67 / 6.67)	1.11	(0.00 / 3.33)	4.33	(0.00 / 8.00)
Large wood debris above active channel (pieces/100 m) - size class 2	0.81	(0.00 / 4.00)	1.24	(0.00 / 7.33)	3.33	(3.33 / 3.33)	0.44	(0.00 / 2.00)	0.75	(0.00 / 2.67)

Large wood debris above active channel (pieces/100 m) - size class 3	0.30	(0.00 / 1.33)	0.57	(0.00 / 4.00)	0.67	(0.67 / 0.67)	0.11	(0.00 / 0.67)	0.08	(0.00 / 0.67)
Large wood debris above active channel (pieces/100 m) - size class 4	0.15	(0.00 / 1.33)	0.19	(0.00 / 1.33)	0.00	(0.00 / 0.00)	0.11	(0.00 / 0.67)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume above active channel (m^3/100 m) - size class 1	1.89	(0.00 / 14.34)	2.20	(0.00 / 14.66)	1.78	(1.78 / 1.78)	0.38	(0.00 / 1.99)	0.50	(0.00 / 1.49)
Large wood debris volume above active channel (m^3/100 m) - size class 2	1.80	(0.00 / 14.15)	1.94	(0.00 / 13.22)	1.58	(1.58 / 1.58)	0.34	(0.00 / 1.91)	0.30	(0.00 / 1.26)
Large wood debris volume above active channel (m^3/100 m) - size class 3	1.55	(0.00 / 12.56)	1.76	(0.00 / 12.32)	0.69	(0.69 / 0.69)	0.28	(0.00 / 1.67)	0.09	(0.00 / 0.69)
Large wood debris volume above active channel (m^3/100 m) - size class 4	1.40	(0.00 / 12.56)	1.17	(0.00 / 8.22)	0.00	(0.00 / 0.00)	0.28	(0.00 / 1.67)	0.00	(0.00 / 0.00)
Large wood debris volume above active channel (m^3/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/100 m) - size class 1	7.19	(0.00 / 19.33)	14.67	(0.00 / 82.67)	24.00	(24.00 / 24.00)	2.11	(0.00 / 6.67)	20.67	(1.33 / 34.00)
Large wood debris in and above active channel (pieces/100 m) - size class 2	1.93	(0.00 / 6.67)	3.05	(0.00 / 17.33)	4.67	(4.67 / 4.67)	0.44	(0.00 / 2.00)	4.33	(0.00 / 10.67)
Large wood debris in and above active channel (pieces/100 m) - size class 3	0.30	(0.00 / 1.33)	1.24	(0.00 / 7.33)	0.67	(0.67 / 0.67)	0.11	(0.00 / 0.67)	0.25	(0.00 / 1.33)
Large wood debris in and above active channel (pieces/100 m) - size class 4	0.15	(0.00 / 1.33)	0.38	(0.00 / 2.67)	0.00	(0.00 / 0.00)	0.11	(0.00 / 0.67)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/100 m) - size class 1	2.52	(0.00 / 15.47)	4.58	(0.00 / 29.06)	3.15	(3.15 / 3.15)	0.44	(0.00 / 1.99)	2.69	(0.08 / 5.30)
Large wood debris volume in and above active channel (m^3/100 m) - size class 2	2.21	(0.00 / 15.23)	3.91	(0.00 / 25.28)	2.03	(2.03 / 2.03)	0.34	(0.00 / 1.91)	1.74	(0.00 / 4.03)

Large wood debris volume in and above active channel (m^3/100 m) - size class 3	1.55	(0.00 / 12.56)	3.39	(0.00 / 22.35)	0.69	(0.69 / 0.69)	0.28	(0.00 / 1.67)	0.26	(0.00 / 1.39)
Large wood debris volume in and above active channel (m^3/100 m) - size class 4	1.40	(0.00 / 12.56)	2.31	(0.00 / 16.17)	0.00	(0.00 / 0.00)	0.28	(0.00 / 1.67)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/100 m) - size class 5	0.00	(0.00 /0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/m^2) - size class 1	0.01	(0.00 / 0.03)	0.01	(0.00 / 0.08)	0.09	(0.09 / 0.09)	0.00	(0.00 / 0.00)	0.06	(0.00 / 0.10)
Large wood debris in active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.02)
Large wood debris in active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/m^2) - size class 1	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.01)
Large wood debris volume in active channel (m^3/m^2) - size class 2	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)
Large wood debris volume in active channel (m^3/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 1	0.01	(0.00 / 0.02)	0.01	(0.00 / 0.05)	0.03	(0.03 / 0.03)	0.00	(0.00 / 0.00)	0.02	(0.00 / 0.03)
Large wood debris above active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.01)	0.02	(0.02 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)

Large wood debris above active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 1	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/m^2) - size class 1	0.02	(0.00 / 0.04)	0.02	(0.00 / 0.13)	0.12	(0.12 / 0.12)	0.00	(0.00 / 0.01)	0.08	(0.00 / 0.12)
Large wood debris in and above active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.03)	0.02	(0.02 / 0.02)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.03)
Large wood debris in and above active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/m^2) - size class 1	0.01	(0.00 / 0.03)	0.01	(0.00 / 0.05)	0.02	(0.02 / 0.02)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.02)
Large wood debris volume in and above active channel (m^3/m^2) - size class 2	0.00	(0.00 / 0.03)	0.01	(0.00 / 0.04)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.01)

Large wood debris volume in and above active channel (m^3/m^2) - size class 3	0.00	(0.00 / 0.03)	0.01	(0.00 / 0.04)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/m^2) - size class 4	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Small wood debris volume in active channel (m^3/m^2)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.01)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.01)
Small wood debris volume above active channel (m^3/m^2)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Small wood debris volume in active channel (m^3/100 m)	0.63	(0.00 / 2.87)	0.75	(0.00 / 4.38)	1.37	(1.37 / 1.37)	0.06	(0.00 / 0.23)	2.01	(0.04 / 4.49)
Small wood debris volume above active channel (m^3/100 m)	0.09	(0.00 / 0.43)	0.27	(0.00 / 1.43)	0.19	(0.19 / 0.19)	0.04	(0.00 / 0.15)	0.21	(0.00 / 0.46)
Channel morphology										
Water flow (m^3/s)	0.12	(0.00 / 0.36)	0.13	(0.00 / 0.45)	0.08	(0.08 / 0.08)	0.16	(0.01 / 0.37)	0.40	(0.05 / 1.05)
Water flow corrected for type of channel bed (m^3/s)	0.10	(0.00 / 0.28)	0.11	(0.00 / 0.36)	0.07	(0.07 / 0.07)	0.13	(0.01 / 0.30)	0.34	(0.05 / 0.84)
Mean water velocity (m/s)	0.02	(0.01 / 0.03)	0.10	(0.06 / 0.16)	0.37	(0.37 / 0.37)	0.54	(0.04 / 2.22)	0.85	(0.17 / 2.17)
SD of mean water velocity (m/s)	0.02	(0.00 / 0.05)	0.08	(0.04 / 0.16)	0.40	(0.40 / 0.40)	0.78	(0.01 / 3.43)	0.32	(0.06 / 1.10)
Depth ratio of bankfull thalweg / thalweg	3.52	(1.69 / 6.30)	3.83	(2.52 / 7.02)	1.91	(1.91 / 1.91)	3.12	(1.96 / 3.86)	2.54	(1.08 / 6.30)
Mean depth of bankfull thalweg (thalweg + bankfull channel height) (m)	1.20	(0.79 / 1.84)	1.19	(0.72 / 1.84)	0.60	(0.60 / 0.60)	1.04	(0.82 / 1.32)	1.40	(0.59 / 3.03)
Ratio bankfull width / bankfull thalweg depth	4.01	(2.66 / 5.62)	6.77	(2.97 / 11.50)	3.24	(3.24 / 3.24)	8.49	(5.10 / 10.50)	2.74	(0.00 / 5.35)

Mean thalweg depth - section (cm)	29.49	(14.58 / 54.95)	23.79	(14.98 / 34.40)	29.02	(29.02 / 29.02)	25.25	(12.60 / 47.11)	48.28	(24.56 / 89.27)
SD of mean thalweg depth - section (cm)	20.98	(11.49/ 33.64)	14.82	(8.74 / 22.13)	22.60	(22.60 / 22.60)	20.71	(9.94 / 32.98)	22.25	(15.10 / 31.52)
Mean thalweg depth (cm)	36.86	(20.28 / 53.45)	32.14	(23.39 / 37.99)	31.45	(31.45 / 31.45)	35.79	(21.30 / 63.12)	62.27	(35.38 / 94.94)
SD of mean thalweg depth (cm)	23.37	(13.39 / 32.19)	16.31	(8.93 / 19.90)	17.93	(17.93 / 17.93)	19.86	(14.80 / 31.85)	18.82	(12.13 / 22.39)
Mean wetted width (m)	3.10	(2.13 / 4.66)	3.52	(2.44 / 4.33)	1.53	(1.53 / 1.53)	3.00	(1.95 / 4.55)	3.12	(0.71 / 10.30)
SD of mean wetted width (m)	1.68	(0.89 / 3.22)	1.67	(0.69 / 2.41)	0.47	(0.47 / 0.47)	1.31	(0.86 / 1.84)	1.12	(0.13 / 5.50)
Mean channel bar width (m)	0.17	(0.00 / 0.65)	0.11	(0.00 / 0.28)	0.00	(0.00 / 0.00)	0.40	(0.23 / 0.70)	0.35	(0.00 / 2.75)
Mean bankfull wetted width (m)	4.61	(2.78 / 5.69)	7.18	(3.89 / 11.21)	1.95	(1.95 / 1.95)	8.54	(6.33 / 9.41)	4.54	(0.00 / 16.20)
SD of mean bankfull wetted width (m)	1.90	(0.63 / 3.56)	1.95	(0.91 / 4.08)	0.45	(0.45 / 0.45)	3.85	(2.21 / 4.98)	1.26	(0.00 / 3.56)
Mean bankfull channel height (m)	0.83	(0.37 / 1.55)	0.87	(0.49 / 1.58)	0.29	(0.29 / 0.29)	0.68	(0.61 / 0.91)	0.77	(0.05 / 2.55)
SD of mean bankfull channel height (m)	0.38	(0.11 / 1.72)	0.54	(0.02 / 1.84)	0.14	(0.14 / 0.14)	0.20	(0.16 / 0.27)	0.32	(0.05 / 1.10)
Mean wetted width x depth - section (m^2)	1.11	(0.31 / 2.25)	0.92	(0.47 / 1.68)	0.51	(0.51 / 0.51)	0.87	(0.29 / 1.48)	1.46	(0.22 / 4.32)
SD of mean wetted width x depth - section (m^2)	1.11	(0.21 / 2.23)	0.79	(0.31 / 1.75)	0.44	(0.44 / 0.44)	0.66	(0.35 / 0.90)	0.60	(0.05 / 2.29)
Mean wetted width / depth - section (m/m)	0.11	(0.07 / 0.22)	0.09	(0.04 / 0.14)	0.17	(0.17 / 0.17)	0.10	(0.06 / 0.16)	0.28	(0.07 / 0.49)
SD of mean wetted width / depth - section (m/m)	0.08	(0.03 / 0.15)	0.07	(0.03 / 0.22)	0.11	(0.11 / 0.11)	0.06	(0.03 / 0.15)	0.13	(0.04 / 0.24)

Mean wetted width x depth (m^2)	1.19	(0.43 / 2.44)	1.15	(0.58 / 1.64)	0.48	(0.48 / 0.48)	1.13	(0.41 / 1.85)	1.86	(0.38 / 4.95)
Mean wetted width / depth (m/m)	8.70	(4.68 / 10.89)	11.08	(7.69 / 16.25)	4.87	(4.87 / 4.87)	8.85	(4.52 / 12.78)	5.71	(1.30 / 21.44)
Mean bank angle (degrees)	41.36	(28.82 / 57.36)	30.99	(28.05 / 36.00)	34.55	(34.55 / 34.55)	34.70	(27.82 / 50.68)	38.75	(0.00 / 62.95)
SD of mean bank angle (degrees)	18.88	(16.16 / 22.07)	14.51	(9.25 / 19.67)	13.88	(13.88 / 13.88)	15.64	(8.86 / 18.55)	12.30	(0.00 / 21.30)
Mean bank undercut distance (m)	0.02	(0.00 / 0.09)	0.02	(0.00 / 0.05)	0.00	(0.00 / 0.00)	0.02	(0.00 / 0.06)	0.02	(0.00 / 0.12)
SD of mean bank undercut distance (m)	0.05	(0.00 / 0.14)	0.06	(0.00 / 0.19)	0.00	(0.00 / 0.00)	0.08	(0.00 / 0.16)	0.05	(0.00 / 0.31)
Mean residual pool depth (m^2/100 m of reach)	26.44	(13.05 / 45.85)	20.10	(11.98 / 26.37)	24.55	(24.55 / 24.55)	25.88	(18.36 / 49.26)	29.13	(19.68 / 48.28)
Mean residual pool depth (m^2/100 m of reach) / Mean thalweg depth (cm)	0.71	(0.61 / 0.88)	0.62	(0.51 / 0.69)	0.78	(0.78 / 0.78)	0.73	(0.60 / 0.86)	0.48	(0.35 / 0.72)
Percent falls	4.52	(0.00 / 19.33)	2.67	(0.00 / 6.00)	0.67	(0.67 / 0.67)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Percent cascade	0.07	(0.00 / 0.67)	0.00	(0.00 / 0.00)	0.67	(0.67 / 0.67)	3.78	(0.00 / 11.33)	2.25	(0.00 / 17.33)
Percent rapids	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	5.67	(0.00 / 31.33)
Percent riffle	39.41	(9.33 / 59.33)	38.76	(21.33 / 58.67)	35.33	(35.33 / 35.33)	0.00	(0.00 / 0.00)	71.92	(14.00 / 100.00)
Percent glide	45.85	(20.67 / 74.67)	56.38	(26.00 / 78.00)	63.33	(63.33 / 63.33)	1.67	(0.00 / 10.00)	18.92	(0.00 / 66.00)
Percent impoundment pool	0.89	(0.00 / 8.00)	1.43	(0.00 / 10.00)	0.00	(0.00 / 0.00)	5.11	(0.00 / 12.00)	0.00	(0.00 / 0.00)
Percent plunge pool	1.70	(0.00 / 15.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	25.78	(2.00 / 44.67)	0.00	(0.00 / 0.00)

Percent lateral scour pool	1.78	(0.00 / 9.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	100.00	(100.00 / 100.00)	0.33	(0.00 / 2.67)
Percent trench pool	5.78	(0.00 / 52.00)	0.76	(0.00 / 5.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.25	(0.00 / 2.00)
Percent bcakwater pool	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	5.78	(0.00 / 21.33)	0.67	(0.00 / 5.33)
Percent dry channel	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	57.89	(32.00 / 98.00)	0.00	(0.00 / 0.00)
Percent falls + cascade + rapids + riffles	44.00	(10.00 / 79.33)	41.43	(21.33 / 64.00)	36.67	(36.67 / 36.67)	3.78	(0.00 / 11.33)	79.83	(34.00 / 100.00)
Percent glides + all pool types	56.00	(20.67 / 90.00)	58.57	(36.00 / 78.67)	63.33	(63.33 / 63.33)	138.33	(102.00 / 156.67)	20.17	(0.00 / 66.00)
Percent all pool types	10.15	(0.00 / 52.00)	2.19	(0.00 / 10.00)	0.00	(0.00 / 0.00)	136.67	(102.00 / 156.67)	1.25	(0.00 / 8.00)
Water flow heterogeneity (fast, smooth, and pool sequence)	0.14	(0.07 / 0.25)	0.14	(0.09 / 0.23)	0.13	(0.13 / 0.13)	0.13	(0.05 / 0.22)	0.02	(0.00 / 0.05)
Fast and slow flow water flow sequence	0.14	(0.05 / 0.25)	0.13	(0.09 / 0.23)	0.13	(0.13 / 0.13)	0.12	(0.04 / 0.19)	0.01	(0.00 / 0.03)
Water surface gradient over reach (%)	0.16	(0.01 / 0.71)	0.08	(0.01 / 0.25)	0.08	(0.08 / 0.08)	0.04	(0.01 / 0.10)	0.05	(0.01 / 0.15)
Channel sinuosity	1.19	(1.07 / 1.33)	1.24	(1.14 / 1.30)	1.20	(1.20 / 1.20)	1.23	(1.11 / 1.35)	1.16	(1.03 / 1.27)

ARTIGO 2

Natural physical-habitat conditions structure fish assemblages of reference streams in a Neotropical drainage

Yuri Malta Caldeira[1,2]; Ruanny Casarim[1]; Paulo dos Santos Pompeu[1]

[1] Setor de Ecologia Aplicada, Departamento de Biologia, Universidade Federal de Lavras, Av. Doutor Sylvio Menicucci 1001, Lavras, Brazil

[2] Correspondent author's e-mail: yurimc86@gmail.com

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Abstract

The structure of freshwater fish assemblages is strongly influenced by aquatic and terrestrial physical habitat characteristics. The natural variation of physical habitat conditions across space is an important driver of fish diversity. High fish diversity of Neoropical river basins is intimately related to the high species turnover among streams. But knowledge on the main natural physical habitat conditions influencing such fish assemblage differentiation is rare, despite its importance for tropical freshwater conservation. In order to fulfill that scientific demand, we tested the hypothesis that landscape- and reach-scale physical habitat conditions are similarly important for fish assemblage structuring of streams in least-disturbed areas of a tropical drainage. We used hand nets to sample fishes and measured 255 physical habitat metrics for 31 streams in five national parks of the Brazilian São Francisco river basin. We included physical habitat metrics of five categories (water chemistry, substrate, fish shelter, riparian vegetation, and channel morphology) along with geographic position and mean elevation of stream reaches in a distance-based linear model (DISTLM) to test which of those best explained the similarity among fish assemblages of streams, calculated based on the Bray-Curtis' index. We visually assessed similarity of fish assemblages and its relation to physical habitat of streams through non-metric multidimensional scaling (NMDS) graphs that had the predictor variables of the best statistically significant linear model as bubble variables. We also performed an analysis of similarity (ANOSIM) and an analysis of similarity percentages (SIMPER) based on similarities of fish assemblages to confirm the separation of streams into groups observed in NMDS graphs and identify the main species related to the differentiation of the groups, respectively. Most of the differentiation among fish assemblages of streams was explained by geographic position (27%), frequency of riffles (14%), flow heterogeneity (6%), and density of woody fish shelter (5%) of stream reaches and was mainly driven by the relative abundance of *Astyanax rivularis* (35%) and *Hisonotus* sp. (13%). We confirmed our hypothesis that natural physical habitat conditions at landscape- and reach-scale have contributions of similar importance to explain the structure of fish assemblages in tropical streams. We also attested that natural mesohabitat configuration and habitat complexity are the most important characteristics structuring ichthyofauna of tropical streams at reach-scale. The present results are novel contributions to science that have the potential to improve the conservation of tropical freshwater fish.

Keywords: reference condition; tropical streams; community structure; fish diversity; ichthyofauna; habitat structure; lotic ecosystem

Resumo

A estrutura das assembleias de peixes de água doce é fortemente influenciada por características aquáticas e terrestres do habitat físico e a variação natural destas no espaço direciona o aumento da diversidade de peixes. A alta diversidade de peixes das bacias hidrográficas neotropicais é intimamente relacionada à pronunciada substituição de espécies entre riachos, ainda assim, o conhecimento sobre as principais condições naturais do habitat físico que influenciam essa diferenciação das assembleias de peixe é escasso apesar da sua importância para a conservação de ecossistemas de água doce tropicais. A fim de suprir essa demanda científica, nós testamos a hipótese de que condições do habitat físico em escala de paisagem e local têm importância similar para estruturação das assembleias de peixe riacho nas áreas menos perturbadas de uma drenagem tropical. Nós usamos peneiras para amostrar os peixes e medimos 255 métricas de habitat físico para 31 riachos em cinco parques nacionais da bacia brasileira do rio São Francisco. Nós incluímos métricas de habitat físico de cinco categorias (química da água, substrato, abrigo para peixe, vegetação ripária e morfologia do canal) juntamente à posição geográfica e elevação média das seções dos riachos em um modelo linear baseado em distância (DISTLM) para testar quais dessa melhor explicaram a similaridade entre as assembleias de peixes de riacho que, por sua vez, foi calculada com base no índice de Bray-Curtis. Nós analisamos visualmente a similaridade entre as assembleias de peixe e sua relação com o habitat físico dos riachos através de gráficos de Escalonamento Multidimensional Não-métrico (*NMDS*) que tiveram as variáveis preditoras do melhor modelo linear estatisticamente significante como variáveis *bubble*. Nós também realizamos uma Análise de Similaridade (*ANOSIM*) e uma análise de Similaridade Percentual (*SIMPER*) baseadas nas similaridades das assembleias de peixe para confirmar a separação dos riachos em dois grupos observados nos gráficos de *NMDS* e identificar as principais espécies relacionadas à diferenciação dos grupos, respectivamente. A maior parte da diferenciação entre as assembleias de peixe dos riachos foi explicada pela posição geográfica (27%), frequência de corredeiras (14%), heterogeneidade de fluxo (6%) e densidade de madeira para abrigo de peixe (5%) dos trechos dos riachos e deveu-se, principalmente, à abundância relativa de *Astyanax rivularis* (35%) e *Hisonotus* sp. (13%). Nós confirmamos nossa hipótese que condições naturais do habitat físico na escala de paisagem e local têm contribuições de importância similar para explicar a estrutura das assembleias de peixe em riachos tropicais. Nós também verificamos que a configuração natural de mesohabitat e a complexidade de habitat são as características mais importantes para estruturação da ictiofauna de riachos tropicais em escala local. Os presentes resultados são contribuições novas para ciência que têm o potencial de aprimorar a conservação de peixes dulcícolas tropicais.

Palavras-chave: condição de referência; riachos tropicais; estruturação de comunidade; diversidade de peixes; ictiofauna; estrutura do habitat; ecossistema lótico.

Introduction

The structure of freshwater fish assemblages is intimately associated to physical habitat conditions. Aquatic fauna is strongly influenced by physical characteristics of waterbodies which constrain living habits and geographic range of species (Jackson *et al*. 2001, Rosenfield 2002, Maceda-Veiga *et al*. 2014). The diversity of fishes in lotic ecosystems depends on a plethora of physical habitat conditions which relative importance for the ichthyofauna vary longitudinally (Vannote 1980) and laterally (Leprieur *et al*. 2011). While the effects of aquatic habitat on fishes are mostly direct and intuitive, the indirect effects of terrestrial habitat are equally important. The average size of riverbed substrate, for example, influence living habits of benthic fish species and it is influenced in turn by the surrounding vegetation which controls bank erosion and fine sediment input into the river (Collins *et al*. 2011, Schwartz *et al*. 2011, Teresa *et al*. 2015). Physical habitat of rivers may also be partitioned into different spatial scales in addition to the aquatic and terrestrial differentiation. Direct and indirect influences of local aquatic and terrestrial habitats are related to the reach-scale while the indirect influences of characteristics such as geology and climate are considered at landscape-scale (Cheek *et al*. 2016). Therefore, management and conservation of fish assemblages in lotic ecosystems must be built on the knowledge of natural relationships between physical habitat and fish assemblages structure at different spatial scales in order to be fully efficient.

Physical habitat conditions naturally vary within pristine areas of drainages promoting fish assemblage differentiation among rivers and consequently increasing fish diversity in the basin. Therefore, the understanding of the natural variation habitats and its consequences to aquatic fauna structuring is essential for setting reference standards for a region (Hughes *et al*. 1986, White & Walker 1997, Kosnicki *et al*. 2014). The establishment of such reference standards is the core of the Reference Condition Approach (RCA) and it is done at different spatial scales depending on size and natural environmental variability of the study area (Lisle *et al*. 2007). The selection of reference sites is a bottleneck of RCA. Ideally, reference sites should be pristine areas that together represent most of the natural variation of the relationships between physical habitat and the fauna in the study area. However, pristine sites are rare in most regions of the world; thus the *a priori* selection of reference sites is usually made in the least-disturbed sites of a region (e.g. protected areas) where most of the natural conditions of the ecosystems may be preserved (Stoddard *et al*. 2006). In developed countries, researchers have broadly discussed and developed the RCA (Hawkins *et al*. 2010, Nestler *et al*. 2010, Bailey *et al*. 2014), and Environmental

Protection Agencies have successfully applied it to improve their methodologies for monitoring, preserving and recovering freshwater ecosystems (Karr 1991, Kaufmann *et al*. 1999, Muxika *et al*. 2007). Meanwhile, most scientists from developing tropical countries do not address the subject despite the great biodiversity and habitat heterogeneity of freshwater ecosystems in their native lands.

The establishment of reference conditions for tropical river basins still is an incipient approach. Tropical regions have some of the largest drainages in the world which encompass diverse physical habitat structures and most of the global freshwater fish diversity (Boulton *et al*. 2008, Lévêque *et al*. 2008). Large tropical rivers usually present high species richness and abundance of migratory species while headwater streams generally have less species but present greater endemism and spatial turnover of species (Winemiller *et al*. 2008). Headwater fish species have limited mobility between streams because of natural biogeographical barriers (Rahel 2007). Therefore, the variation of local physical habitat conditions of streams is directly related to differences among fish assemblages of streams and, in consequence, partially responsible for the diversity of fishes in a basin (Heino *et al*. 2015). Nevertheless, there are few studies on the natural variation of physical habitat conditions of tropical streams and its consequence on the structuring of fish assemblages. Most studies on tropical stream fishes focus on the impact of anthropic physical habitat alterations (e.g. deforestation, agriculture, and impoundment) on assemblages (Lorion & Kennedy 2009, Terra *et al*. 2013, Teresa *et al*. 2015). The presence of top research centers and universities in tropical areas with intense human interference might be a reason for that. But the intensity of human impacts on tropical streams is also a reason that makes research on RCA a relevant subject. Examples from temperate regions have shown that the establishment of reference standards is essential for efficient conservation practices (White & Walker 1997, Bilotta *et al*. 2012, Grove *et al*. 2015). Therefore, scientists from tropical countries with abundant freshwater and great fish diversity, such as Brazil, should have a leading role in that field.

The study of Brazilian reference streams is both a challenge and a necessity. Some of the largest tropical rivers in the world are present in Brazil (Latrubesse *et al*. 2005). The large territory of the country also holds many different landscapes and biomes, some of which are considered biodiversity hotspots (Myers *et al*. 2000). Unfortunately, the natural conditions of those ecosystems are obscured by the effects of human interference. While large lotic ecosystems are mainly threatened by impoundments, wadeable streams impacts are often related to habitat alterations by agriculture, livestock farming and other economic activities (e.g. mining) (Agostinho *et al*. 2005). Southeast Brazil is the most populated, economically developed, and human modified region of the country (Azzoni 2001). The region was originally occupied by Cerrado and Atlantic Forest landscapes but most of the original cover has been removed (Klink & Machado 2005, Ribeiro *et al*. 2009), and the least-disturbed areas of both biomes are now mainly restricted to legally-protected areas. Nevertheless, the drainages of the region present high gamma diversity of fishes (Alves *et al*. 2011, Langeani *et al*. 2007) mainly because of the generally high species turnover among streams that make regional beta diversity high (Winemiller *et al*. 2008). Thus, the study of the natural relationships between physical habitat conditions and fish assemblages in the protected areas should improve the knowledge on reference conditions of streams and on the drivers of tropical streams beta diversity.

In this study, we tested the hypothesis that geographic position (landscape sacle) and physical habitat characteristics (local scale) of refrence streams would have similar importance for the differentiation of fish assemblages, in order to better understand the natural fish species turnover among tropical streams. We measured multiple physical habitat variables at reach-scale to account for most of the local influences on fish assemblages and used geographic position of streams to summarize the influence of biogeographical processes and landscape-scale variables (e.g. geology) that were not individually quantified in our study. The identification of the most relevant beta diversity drivers among physical habitat characteristics may improve the conservation of tropical fishes.

Material and methods

Study area

The São Francisco river basin is one of the most important drainages in Brazil. It drains an area of 645067.2 km^2 and it is the largest basin entirely located in Brazil (Godinho & Godinho 2003). The São Francisco river runs through five states and the upper and part of middle regions of its basin occupy approximately 40 % of Minas Gerais state area. The two main biomes in the basin are the Cerrado and Caatinga (Alves & Leal 2010). In Minas Gerais, Cerrado is predominant in the upper region of the basin while in the middle course there is an ecotone between Cerrado and Caatinga. Additionally, the basin is known because of its importance for inland fisheries and its large fish species richness (Godinho & Godinho 2003): 208 native and 16 exotic fish species have been registered (Alves *et al*. 2011). A total of 493723.27 ha of São Francisco river basin in Minas Gerais are protected by five national parks (PARNA): Serra da Canastra, Serra do Cipó, Sempre-Vivas, Grande Sertão Veredas, and Cavernas do Peruaçu (Figure 1). 'National park' is one of the protected areas categories with most restrictive use in Brazilian legislation (SNUC 2000), thus national parks are considered some of the best-preserved natural areas in Brazil.

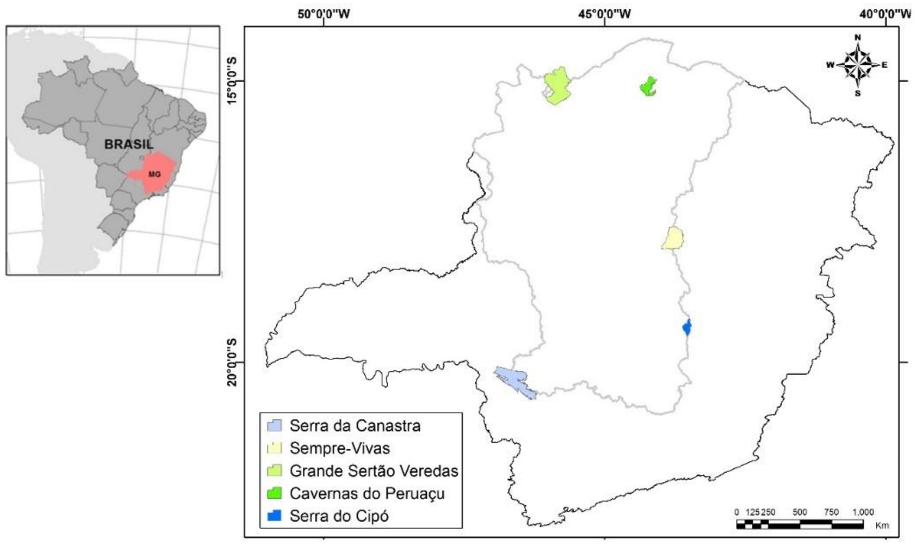

Figure 1. Study area in the São Francisco river basin in Minas Gerais. Physical habitat metrics and fishes of reference streams were sampled in the following national parks (PARNA): PARNA Serra da Canastra, PARNA Sempre-Vivas, PARNA Grande Sertão Veredas, PARNA Cavernas do Peruaçu, and PARNA Serra do Cipó. The light grey line delimitates the São Francisco river basin in Minas Gerais and PARNAs are identified by colors as defined in the figure.

PARNA Serra da Canastra is located in southwestern Minas Gerais and has an area of 197787 ha. The park was established in 1972 and it is one of the main federal areas for the protection of the Cerrado, a biodiversity hotspot. The park and its surrounding area encompass 581.7 km^2 of the São Francisco river basin in which were registered 22 fish species (MMA/IBAMA 2005a).

PARNA Serra do Cipó is located in the central region of Minas Gerais and has an area of 31617.8 ha. The park was established in 1984 (ICMBio 2009) and it includes areas of two highly threatened biomes: Cerrado and Atlantic Forest. The Espinhaço Complex mountain range, that runs across the park, separates the São Francisco from the Brazilian East Atlantic costal drainages (Alves et al 2008). Also, the park includes almost all the headwaters of the Cipó river. This river is one of the best-preserved tributaries of the Velhas river, one of the largest rivers that run to the São Francisco river in the upper region of the basin. In the park, Vieira *et al*. (2005) registered 15 fish species for the Cipó river and its tributaries.

PARNA Sempre-Vivas is located between Minas Gerais central and northern regions and it accounts for an area of 124154.47 ha. The park was established in 2002 and it includes areas of Cerrado and Atlantic Forest areas. This PARNA is also located in the Espinhaço Complex mountain range which separates the São Francisco from the Jequitinhonha river drainage in this region. So far, there are no ichthyofaunal surveys in the Park area (MMA/ICMBio 2014).

Grande Sertão Veredas National Park is located in the northern region of Minas Gerais and it has an area of 83364 ha. The park was established in 1989 and it has six different Cerrado physiognomies in its area. Also, the abundance of arenites in the soil of the park allows it to hold a great amount of water in perennial rivers and peculiar ecosystems known as ‘veredas’. The water bodies of the park belong to the Carinhanha and Urucuia rivers drainages. Both rivers are important tributaries on the left margin of the São Francisco river. In those drainages, a total of 62 fish species were registered in the park when considering rivers, lagoons, streams, and ‘veredas’ (MMA/IBAMA & FUNATURA 2003).

Cavernas do Peruaçu National Park is located in the northern region of Minas Gerais and it encompasses an area of 56800 ha. The park was established in 1999 and its region is an ecotone between Cerrado and Caatinga. In the park, there are few superficial and perennial lotic environments, an exception being the Peruaçu river, an important tributary of the São Francisco River due to its perennial flow in a region of dry climate. But despite the importance of Peruaçu river, there is still little knowledge on the basin’s fish fauna in the region of the park (MMA/IBAMA 2005b).

Data sampling

We sampled 31 second or third order streams (Strahler 1957) inside the five PARNA previously mentioned. From September to October of 2014, we sampled seven streams in PARNA Serra do Cipó and nine in PARNA Serra da Canastra. In April of 2015, we sampled one stream in PARNA Cavernas do Peruaçu, eight in PARNA Grande Sertão Veredas, and four in PARNA Sempre-Vivas. We returned to PARNA Sempre-Vivas in October 2015 and sampled two additional streams. All sampling occurred at the end of the dry season, considered the best period for the stream characterization (Kaufmann et al. 1999), but this reduced the number of streams with flowing water that could be sampled. We selected streams based on the presence of water and our capacity to access them.

We sampled physical habitat of streams following the methods described by Peck *et al*. (2006) and Hughes and Peck (2008). We delimitated a 150 m long reach at each stream and divided it in ten 15 m long transects using 11 cross-sections. We took depths measurements and evaluated the presence of fine sediment at ten equally distant points along each transect. We visually determined the type of flow at each transect point and counted the number of channel bars, wood debris in the bankfull stage channel, lateral channels, and backwater pools along the transect. We used a compass and estimated the percentage length of the reach running in each direction to determine changes in flow direction and sinuosity.

We characterized the habitat of the stream channel and riparian zones at each cross-section. We first measured the depth and visually determined the type of substrate and its immersion at five points equally distant along the cross-section. We measured the canopy cover over the channel and banks using a convex spherical densiometer (Lemmon 1957). We visually determined and quantified the abundance of potential fish shelters (algae, macrophytes, wood debris, tree roots, leaf banks, overhanging vegetation, undercut banks, boulders, artificial structures) 5 m upstream and downstream from each cross-section. We measured bank angle with a clinometer and used a measuring tape for undercut banks length, channel wetted width, channel bars width, channel height and width at bankfull stage, and channel incision height. We characterized the riparian vegetation based on a 10-m^2 quadrat on each bank. The quadrats extended 5 m upstream and 5 m downstream from the cross-section and we visually estimated the percentage cover of each type of vegetation for the canopy layer, understory, and ground cover layer. We also visually identified potential human impacts (e.g. pasture, agriculture, and mining) in the area and estimated their distance from the banks. We used a GPS to obtain the elevation, latitude, and longitude of the points at the ends of the reach and used the difference in elevation to calculate reach slope. We also used elevation data from both ends of each reach to calculate its mean elevation. Latitude and longitude of the upstream-end of the reach were combined to determine the geographic position of the reach.

We measured water chemistry parameters at the end or beginning of the reach before sampling physical habitat metrics. We used a multiparameter water quality probe to measure water pH, conductivity, temperature, and dissolved oxygen. We took measurements right below water surface at the center point of the cross-section of the stream.

After the characterization of the physical habitat of the stream, we sampled fishes for 120 minutes. We maintained the same transects established for habitat characterization during fish sampling and each transect was sampled for 12 minutes. Two people used semi-circular hand nets with 0.8 m in diameter and 2 mm stretched mesh size to sample fish. We only used hand nets because they are efficient in most low-order streams. Other sampling gear (e.g. seine) are not suitable for some habitat, therefore using them would difficult comparisons among fish assemblages of reference streams. Then, we sacrificed all sampled fishes in anesthetic Eugenol solution and fixed them in 10% formalin. In laboratory, we transferred fishes to 70% ethanol, identified them to the species level, and determined the fish assemblages of streams.

Data analysis

We calculated 255 physical habitat related metrics from the field sampling data following Peck *et al*. (2006) and Hughes and Peck (2008). We used the data from the field to produce 36 substrate metrics, 35 fish shelter metrics, 101 riparian vegetation metrics, 48 channel morphology metrics, 29 human impact metrics, and six water chemistry metrics (S1). Out of this 255 metrics, we selected eight for substrate, eight for fish shelter, 14 for riparian vegetation, 17 for channel morphology, and four for water chemistry based on the results of correlation analyses between metrics (one metric excluded when correlation was statistically significant and the coefficient greater than 75%) and the recurrence of metrics (or equivalent metrics) in different habitat assessment protocols. We excluded human impact metrics from analyses because we were only interested on the natural variations of the physical habitat of streams and human interference inside national parks was generally restricted to low-impact tourism (e.g. trails).

We used distance-based linear models (DISTLM) to test if geographic position and physical habitat characteristics of streams would explain the fish composition variation among those streams. We performed a DISTLM analysis using fish species composition of the streams as the response variable and physical habitat metrics, mean elevation, and geographic position of streams as explanatory variables. In the explanatory matrix, we grouped the latitude and longitude (UTM) of the initial point of the reach to serve as proxy for the geographic position of streams and we chose the Bray-Curtis's similarity index for the fish assemblage matrix because it is an appropriate method for species abundance data. We identified statistically significant explanatory variables through marginal tests. For the models, we used the forward selection. In both cases we adopted a 0.05 significance value. The best model was the one with greatest adjusted-R^2 among the statistically significant ones.

We visually assessed the similarity among fish assemblages of reference streams by non-metric multidimensional scaling (NMDS) and further investigated the pattern that each of the most influential physical habitat characteristics (identified in the DISTLM analysis) followed in the given distribution of streams. We used Bray-Curtis' similarity index to compare fish assemblages of reference streams. The accuracy of the representation of streams similarity in the 2D-graph was verified through the Kurskal stress formula with a minimal stress of 0.01 Then, we reproduced the resulting graph once for each of the important physical habitat metrics and we used them as indicator (categorical) or bubble (continuous) variables. Additionally, we tested the statistical significance (0.05 significance value) of potential groups of streams visually detected in the NMDS graph with an analysis of similarity (ANOSIM) with 999 permutations and followed it with a similarity percentages (SIMPER) analysis to measure the within and between groups similarity among fish assemblages of reference streams. We also used the SIMPER analysis to identify the fish species that most contributed for 90% of the dissimilarity between assemblages of the groups. Once again, we used the matrix built on the Bray-Curtis' similarity index for assemblages of streams in both ANOSIM and SIMPER analyzes. We performed all the analyzes in the software Primer+Permanova (Clarke & Gorley 2006).

Results

Fish species composition varied greatly among fish assemblages of refrence streams in the São Francisco river basin. A total of 4297 individuals of 50 different species were sampled (S1). Reference streams with most and least sampled individuals had 1112 and zero sampled fishes, respectively. The most species-rich stream had 19 different fish species and it was located in PARNA

Grande Sertão Veredas. There were no sampled individuals in four streams: two in PARNA Serra da Canastra and two in PARNA Sempre-Vivas. *Astyanax rivularis* was the most sampled species in number of individuals (3087) and number of streams (21). On the other hand, 19 fish species had from one to seven individuals sampled and occurred in only one stream. PARNA Serra da Canastra had more sampled individuals and PARNA Cavernas do Peruaçu had the least (1848 and 230, respectively). However, PARNA Grande Sertão Veredas was the most species-rich region with a total of 35 different sampled fish species. PARNA Cavernas do Peruaçu and PARNA Sempre-Vivas were the regions with least sampled species: six species each.

Physical habitat conditions also presented great variation among reference streams and parks (S2). Metrics such as ‘percentage of channel’s substrate average immersion’, ‘percentage of substrate with diameter < 16 mm’, ‘total areal cover for fish’, ‘riparian canopy and mid-layer cover’, and ‘mean thalweg depth - section’ had a wide range of values among streams in the same park. Also, metrics such as ‘water conductivity 1’, ‘percentage of fine’, ‘filamentous algae areal cover’, ‘riparian canopy and mid-layer cover’, and ‘percent riffle’ had great variation of mean values between parks.

Geographic position, frequency of riffles, flow heterogeneity, and abundance of woody fish shelter of reference streams explained most of the variation observed for fish assemblages. Although 26 physical habitat characteristics individually had statistically significant relationships with fish assemblages of streams (Table 1), only four of those were part of the best statistically significant model of the DISTLM analysis (Table 2). In that model, geographic position, frequency of riffles, flow heterogeneity, and abundance of woody fish shelter of streams explained 52% of the variation in fish species composition (adjusted $R^2 = 0.52$; $P < 0.05$) (Table 2).

Table 1. Relationship between selected physical habitat characteristics and fish assemblages of reference streams. The present results for the marginal tests of the DISTLM analysis only include habitat metrics that presented statistically significant (P-value < 0.05) relationships with fish assemblages.

Variables	**Pseudo-F**	**P-value**	**Proportion of explanation**
Mean elevation (m)	2.20	< 0.05	0.08
Geographic position	4.24	< 0.01	0.27
Total areal cover for fish except filamentous algae and aquatic macrophytes	3.00	0.01	0.11
Abundance of woody fish shelter (large and small woody debris areal cover)	7.99	< 0.01	0.25
Root areal cover	3.30	0.01	0.12
Leaf bank areal cover	2.59	0.03	0.10
Dissolved oxygen (mg/L)	2.22	0.04	0.08
Mean canopy density mid-stream (%)	4.17	< 0.01	0.15
Mean canopy density at bank (%)	3.43	0.01	0.13
Riparian canopy and mid-layer cover	7.29	< 0.01	0.23
Large wood debris above active channel (pieces/m2) - size class 1	2.64	0.03	0.10
Large wood debris in and above active channel (pieces/m2) - size class 1	3.37	0.01	0.12

Large wood debris in and above active channel (pieces/m2) - size class 2	2.91	0.01	0.11
Mean wetted width / depth (m/m)	2.62	0.03	0.10
Fast and slow flow water flow sequence	2.89	0.02	0.11
Flow heterogeneity (fast, smooth, and pool)	2.97	0.01	0.11
Percent glides + all pool types	7.54	< 0.01	0.24
Percent glide	5.52	< 0.01	0.24
Frequency of riffles (percent riffle)	8.50	< 0.01	0.26
Percent falls + cascade + rapids + riffles	7.58	< 0.01	0.24
Channel sinuosity	2.74	0.02	0.10
Small sediment on channel bed (%)	6.07	< 0.01	0.20
channel's substrate average immersion (%)	5.34	< 0.01	0.18
Mean substrate size	4.41	< 0.01	0.16
Log10 [relative bed stability]	2.44	0.03	0.09
Substrate > 16 mm diameter (%)	4.55	< 0.01	0.16

Table 2. Relationship between fish assemblages of reference streams and their respective geographic position, frequency of riffles, flow heterogeneity, and abundance of woody fish shelter. The best significant (P < 0.05) DISTLM model is presented.

Variables	**Adjusted R^2**	**Pseudo-F**	**P-value**
Geographic position	0.27	4.24	< 0.01
+ Frequency of riffles (percent riffle)	0.41	5.15	< 0.01
+ Flow heterogeneity (fast, smooth, and pool)	0.47	2.48	0.01
+ Abundance of woody fish shelter (large and small woody debris areal cover)	0.52	1.87	< 0.05

The visual analysis of the similarity of fish assemblages of reference streams corroborated the previously attested influence of geographic position on fish species composition (Figure 2). PARNA Grande Sertão Veredas presented the greatest variation of species composition among streams. Streams in the Espinhaço Mountain Range (PARNA Serra do Cipó and PARNA Sempre-Vivas), most streams in PARNA Serra da Canastra, and the stream in PARNA Cavernas do Peruaçu had similar species composition. Thus, the streams could be separated into two uneven groups based on the NMDS plot: the first one (‘a’) would have streams with more similar fish assemblages and it would include all the streams from the Espinhaço Mountain Range, all but two streams from PARNA Serra da Canastra, three streams from PARNA Grande Sertão Veredas, and the one stream from PARNA Cavernas do Peruaçu; the second group (‘b’) would have less similar fish assemblages and it would include five streams from PARNA Grande Sertão Veredas and two streams from PARNA Serra da Canastra.

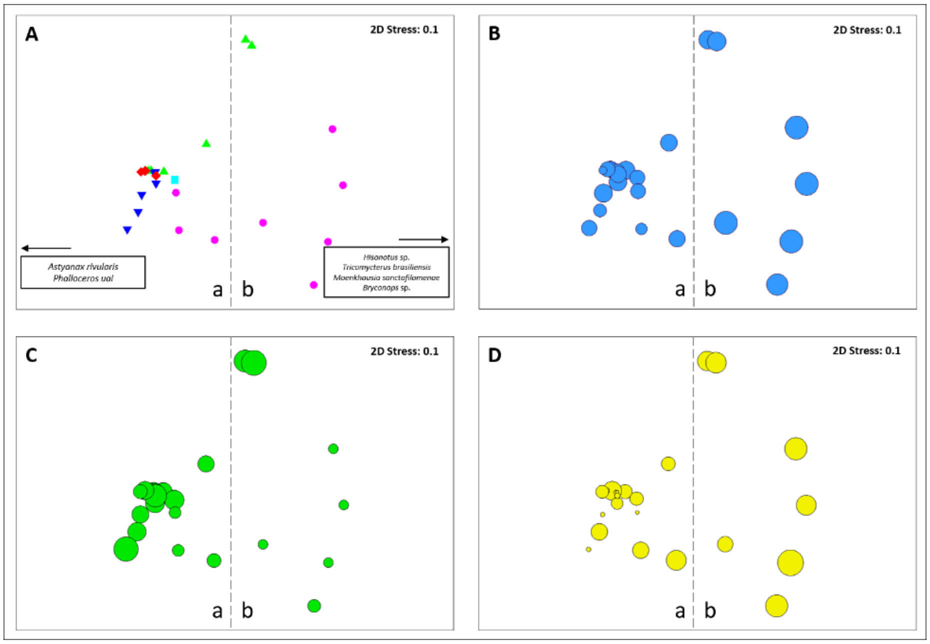

Figure 2. Similarity analysis of fish assemblages of (**A**) geographic position, (**B**) frequency of riffles, (**C**) flow heterogeneity, and (**D**) abundance of woody fish shelter of reference streams. The 2-D representation of the similarity of reference streams was adequate (Stress = 0.10) and streams were visually separated into groups 'a' and 'b' in the NMDS-graphs. The separation of groups 'a' and 'b' was statistically confirmed (ANOSIM, global R = 0.89; P < 0.01) and the species that best characterized each group (see Table 3) are shown inside boxes in graph **A**. Geographic position of streams is represented in graph **A** as follows: light blue square = Cavernas do Peruaçu National Park; pink circle = Grande Sertão Veredas National Park; red diamonds = Sempre-Vivas National Park; green triangles = Serra da Canastra National Park; upside-down blue triangles = Serra do Cipó National Park. In graphs **B**, **C**, and **D**, symbol sizes are directly proportional to the values of frequency of riffles, flow heterogeneity, and abundance of woody fish shelter, respectively.

Reference streams in group 'a' generally had less frequency of riffles, greater flow hetereogeneity, and less woody fish shelter than streams in group 'b' (Figure 2). Nevertheless, the high flow heterogeneity of the two streams from PARNA Serra da Canastra in group 'b' and the generally low heterogeneity for streams from PARNA Grande Sertão Veredas in both groups were remarkable.

Additionally, the average abundance of woody fish shelter in streams belonging to group ‘a’ was notably lower than that of streams in group ‘b’.

The fish species that allowed the differentiation of the groups in ANOSIM (global $R = 0.89$; $P < 0.01$) were identified. *Astyanax rivularis* was the species the best characterized fish assemblages of streams in group ‘a’ and its average abundance was the major difference between fish assemblages of groups ‘a’ and ‘b’ (Table 3). On the other hand, *Hisonotus* sp. was the most representative species of fish assemblages of streams in group ‘b’ and its abundance was the second most important for the dissimilarity between the groups. *Trichomycterus brasiliensis*, *Moenkhausia sanctafilomenae*, and *Bryconops* sp., which were more representative for streams in group ‘b’, and *Phalloceros uai* that was more representative for streams in group ‘a’, also had important contributions for the dissimilaritiy between groups.

Table 3. Dissimilarities between groups ‘a’ and ‘b’ based on the fish composition of reference streams. Astyanax rivularis and Hisonotus sp. were the species that best characterized groups ‘a’ and ‘b’, respectively. Average abundance in streams of both groups and contribution to the overall dissimilarity between groups is presented for the species that together contributed to 90% of the between groups dissimilarity according to the SIMPER analysis. Average within groups similarities among streams: ‘a’ = 76.64; ‘b’ = 56.01. Average between group dissimilarity of streams was 48.15.

Fish species	**Group ‘a’ average abundance**	**Group ‘b’ average abundance**	**Dissimilarity contribution (%)**	**Cumulative dissimilarity contribution (%)**
Astyanax rivularis	34.16	0.73	34.71	34.71
Hisonotus sp.	0.50	12.62	13.03	47.74
Trichomycterus brasiliensis	1.31	10.60	11.59	59.33
Moenkhausia sanctafilomenae	0.00	6.30	6.54	65.87
Bryconops sp.	0.00	5.04	5.24	71.11
Phalloceros uai	4.83	0.00	5.02	76.13
Eigenmannia gr. *trilineata*	0.00	2.20	2.28	78.41
Cetopsorhamdia iheringi	0.10	2.19	2.27	80.68
Harttia sp. 1	0.21	2.01	2.24	82.92
Trichomycterus variegatus	0.26	1.13	1.33	84.25
Characidium cf. *zebra*	1.05	0.34	1.33	85.58
Phenacogaster franciscoensis	0.94	0.42	1.32	86.90
Hypostomus sp. 2	0.40	0.80	1.13	88.03
Astyanax fasciatus	0.89	0.13	1.03	89.06
Piabina argentea	0.87	0.00	0.90	89.96
Pareiorhina cepta	0.17	0.71	0.87	90.84

Discussion

Geographic position, frequency of riffles, flow heterogeneity, and abundance of woody fish shelter were able to explain most of the fish composition variation among reference streams in the São Francisco river basin. We confirmed our hypothesis that landscape- and local-scale habitat characteristics had similar importance for the natural structuring of fish assemblages. Fish assemblages of streams were naturally determined by landscape constraints (geographic position), water flow characteristics (frequency of riffles and flow heterogeneity) and habitat complexity (abundance of woody fish shelter). Geographic position of streams accounted for biogeographical and natural environmental differences among regions of the basin. Additionally, water flow and fish shelter were the local habitat characteristics that explained the variation in fish assemblages once the geographic position of the streams had been considered.

The effects of geographic position, frequency of riffles, flow heterogeneity, and abundance of woody fish shelter also accounted for the influence that other physical habitat characteristics individually had on the differentiation of fish assemblages of reference streams. Twenty-six out of 47 physical habitat correlated to differences in fish assemblages among streams when habitat metrics were considered one at a time. Nevertheless, the variation of most of those physical habitat metrics were not considered good explanations for the differences in fish assemblages among streams when all habitat metrics were considered together. The reason for it was that each of the four physical habitat metrics selected as good explanatory variables (i.e. geographic position, frequency of riffles, flow heterogeneity, and abundance of woody fish shelter) were probably efficient proxies of the effects of the other 22 meaningful metrics. Geographic position of streams probably represented part of the variation of most physical habitat metrics because regional geology, climate, hydrology, and phytophysiognomy are important constraints for streams' substrate, water chemistry, channel morphology, riparian vegetation, and fish shelter (Covich *et al*. 2003, Bailly-Comte *et al*. 2009, Teresa & Romero 2010, Grove *et al*. 2015, Amuchástegui *et al*. 2016). Furthermore, geographic position must also have accounted for the influence that mean elevation of streams had on fish assemblages because mean elevation of streams was lower in the middle region of the São Francisco river basin (i.e. PARNA Cavernas do Peruaçu and PARNA Grande Sertão Veredas) than in the upper region (i.e. PARNA Serra da Canastra, PARNA Serra do Cipó, and PARNA Sempre-Vivas). Frequency of riffles probably was a proxy for the effects of similar (e.g. frequency of fast flow) and antagonistic (e.g. frequency of slow flow) metrics, and also for metrics which values are commonly associated to the type of mesohabitat (e.g. substrate average size, average leaf bank shelter, and dissolved oxygen concentration) (Martin-Smith 1998, Schwartz & Herricks 2008). Flow heterogeneity also probably represented the influence of similar (e.g. fast and slow flow sequence) and flow-related (e.g. small sediment on the thalweg, relative bed stability, and section's sinuosity) metrics (Kano *et al*. 2013, Schwartz *et al*. 2015). Finally, wood debris were the main type of fish shelter present in reference streams and its instream abundance is directly influenced by the surrounding phytophysiognomy (Kreutzweiser *et al*. 2005). Hence, the density of woody fish shelter probably incorporated the relationships that the metric of average total fish shelter and metrics related to the riparian vegetation (e.g. average canopy cover over channel, density of class 1 wood debris above channel, and average tree root fish shelter) had with fish assemblages of streams.

Environmental conditions at the landscape-scale and regional species pool were possibly the main factors related to the geographic position of reference streams that influenced the variation of fish assemblages. Stream reaches were distributed over a large area with regional variability in geology, geomorphology, and climate (Pereira *et al*. 1994, Saadi 1995, Alves & Leal 2010, Fragoso *et al*. 2011). Those macro environmental features act as filters that limit which fish species are present in each region of a river basin (Heino *et al*. 2015). Historical patterns of those conditions are important determinants of speciation and species colonization, extinction, and dispersal (Magnuson *et al*. 1998, Olden *et al*. 2010). Natural modifications of the relief may alter the connectivity between water bodies which may promote speciation through vicariance or expansion of the distribution of some species, for example (Burridge *et al*. 2006). Additionally, temperature fluctuations and soil minerals may indirectly determine and modify the geographic range of species by influencing landscape characteristics such as phytophysiognomy and substrate profile (Grenouillet *et al*. 2002, Moyle *et al*. 2003, Hough-Snee *et al*. 2015). Thus, those landscape aspects are relevant determinants of the biogeography of stream fishes. In the studied area of the São Francisco river basin, the biogeography of fishes was the first and most important factor to determine the fish composition of reference streams. That result corroborates the idea that landscape-scale effects are more relevant for species distribution than local-scale habitat characteristics for the analysis of large areas (Esselman & Allan 2010, Pease *et al*. 2012). Nevertheless, reference streams under the influence of the same landscape conditions still presented differences in fish composition in the São Francisco river basin. Therefore, natural variation of local habitat characteristics among streams also contributed for the differentiation of fish assemblages at a finer spatial scale.

Frequency of riffles and flow heterogeneity were important local habitat variables for the differentiation of fish assemblages among reference streams in the São Francisco river basin. Differences in the adaptation of fishes to local physical habitat conditions affect the composition of fish assemblages of reference streams. Local habitat conditions of streams directly influence shelter, feeding, and reproduction of fishes (Mitchell *et al*. 2012, Espírito-Santo *et al*. 2013, Kano *et al*. 2013). Many of those local features merely represent the indirect effects of landscape-scale variables on fish composition (Rowe *et al*. 2009). Nevertheless, the variation of some local habitat features among streams are enough to promote additional fish assemblage differentiation (Cheek *et al*. 2016). Riffles are mainly characterized by faster water flow and coarser substrate than pools (Schwartz *et al*. 2015). Additionally, riffles are often shallower and therefore have more algae and vegetation growth than pools (Martin-Smith 1998). In our study, streams with greater frequency of riffles had greater abundance of *Hisonotus* sp., *Trichomycterus brasiliensis*, and *Bryconops* sp., three rheophilic fish species. Rheophilic species present various adaptations to live in riffles: *Hisonotus* sp. has a vertically depressed body that increases its hydrodynamic and a sucking mouth that helps it adhere to the instream vegetation (Casatti & Castro 2006, Kadye & Moyo 2008, Sagnes & Statzner 2009); *T. brasiliensis* was mostly found associated to coarse substrate such as gravel and boulders. Its body is long and cylindrical, and its head is slightly depressed both of which make it a hydrodynamic bottom dwelling fish (Meyers & Belk 2014). It also has opercular spines that help it cling to the substrate to avoid being washed away (Adriaens *et al*. 2010); *Bryconops* sp. lives in the water column and its elongated and robust body make it well-adapted to swim against the water current (Langerhans *et al*. 2003).

On the other hand, reference streams with less frequency of riffles generally had greater water flow heterogeneity therefore they also had greater frequency of slow flowing conditions. Habitats with slowing flowing water are usually deeper and present reduced average substrate size due to the greater deposition of fine sediment on the stream bottom (Martin-Smith 1998). Therefore, bottom dwelling fishes are not as predominant in those habitats as they are in riffles and there are usually more nektonic species associated with slow water flows (Greenberg 1991, Rezende *et al*. 2010). In our study, most reference streams with greater flow heterogeneity had greater abundance of *Astyanax rivularis* and *Phalloceros uai*, two nektonic fish species. *A. rivularis* was present in 20 of the

26 sampled streams and it was the fish species with widest distribution. Its abundance was greatest in streams with greatest flow heterogeneity though. The body shape of *A. rivularis* is adapted for swimming in different layers of the water column and individuals of the species were commonly sampled in habitats with fast and with slow water flows although the species does not have obvious morphological adaptions to high water velocities (Casatti & Castro 2006). Contrastingly, *P. uai* was sampled in only four reference streams and the individuals were sampled near the margins of the streams in slow flowing water conditions. The species small size, deep and laterally depressed body, and large fins give the individuals good maneuverability in slow flow conditions but make them poorly adapted to fast water flow (Leal *et al*. 2011). Thus, habitat conditions constrained the presence and influenced the abundance of fish species inhabiting reference streams because species have adaptations for specific conditions. Hence, the natural variation of local physical habitat conditions in the São Francisco river basin contributed for the differentiation of fish assemblages among reference streams.

In our study, reference streams with greatest abundance of wood debris for fish shelter were also the ones with greatest frequency of riffles and were mostly located in PARNA Grande Sertão Veredas and PARNA Serra da Canastra. Wood debris alter local physical conditions and create microhabitats suitable for some fish species. Presence of large wood debris (e.g. tree trunks) in headwater streams is directly related to the riparian vegetation profile because streams rarely have water flows with enough power to carry large wood debris downstream (Cordova *et al*. 2007). Thus, reference streams with high abundance of woody fish shelter also had dense canopy cover such as the streams of 'veredas' in PARNA Grande Sertão Veredas and the riparian forests in low-elevation streams in PARNA Serra da Canastra. Wood debris increase instream habitat complexity and provide hard surfaces that serve as shelter and foraging substrate for aquatic fauna (Oliveira *et al*. 2016). The higher abundance of *Hisonotus* sp. in reference streams with more woody fish shelter was probably linked to the living habits of the fish: individuals of that species were usually associated to submerged vegetation close to the streambanks, but they were also common on submerged wood debris. Submerged vegetation and wood debris create microhabitats with slower water flow and hard surfaces which reduce the energy spent by *Hisonotus* sp. and give it a substrate upon which it can scrape its food, respectively (Jackson *et al*. 2001, Teresa & Casatti 2012, Casatti & Castro 2006). The reduced water velocity in the microhabitats created by large wood debris may also be important for the greater abundance of *Moenkhausia* *sanctaefilomenae* in reference streams with more woody fish shelter. This nektonic fish species is adapted to lotic environments but its deep and laterally depressed body is more suitable for slow water flow conditions (Casatti & Castro 2006, Padial *et al*. 2009). Therefore, the microhabitats created by large wood debris were probably important for the maintenance of *M. sanctaefilomenae* populations in the reference streams with high frequency of riffles. Additionally, wood debris may also have held plants and invertebrates upon which *M. sanctaefilomenae* fed. Hence microhabitats created by wood debris also stimulated the differentiation of fish assemblages of reference streams.

Studies on the relationship between fishes and physical habitat of streams in other regions concur with our results for reference streams in the São Francisco river basin. Those studies also attested mixed influences of local and landscape variables on stream fauna, although influential habitat characteristics varied among regions and studied group of organisms (Wang *et al*. 2006, Ferreira *et al*. 2014, Cheek *et al*. 2016, Milner *et al*. 2015). Some research focused on the influence of local habitat variables (Poff & Allan 1995, Schwartz & Herricks 2008, Cianfrani *et al*. 2009, Mitchell *et al*. 2012) while others highlighted the effects that landscape variables on fish assemblages (Tonn 1990, Pedersen *et al*. 2004, Hough-Snee *et al*. 2015). But most studies compared the influence of habitat variables at different spatial scales on the structuring of stream fish assemblages (Smith & Kraft 2005, Rowe *et al*. 2009, Pease *et al*. 2012, Heino *et al*. 2015). These studies generally attested that reach-scale variables were the more influential ones (Cheek *et al*. 2016) and some authors argued that landscape variables would only be important influences in systems with high levels of anthropogenic modification (Wang et al. 2003). Although we did not measure the influence of individual landscape variables, our results contradicted those authors by suggesting that landscape- (i.e. geographic position) and reach-scale (i.e. frequency of riffles, flow heterogeneity, and abundance of woody fish shelter) characteristics had equivalent importance to determine the structure of fish assemblages of areas under little human influence. Esselman and Allan (2010) also had results similar as they observed that landscape variables had greater influence on fish assemblages than reach-scale variables for small rivers in moderately disturbed areas. The authors suggested that the large variation of landscape characteristics and the presence of different biogeographic regions in their study area could possibly explain why their results contradicted previous studies. The same may apply to our work because the large geographic extent of our study area contemplated least-disturbed regions in varying landscapes and different sub-basins of the São Francisco river basin. Thus spatial scale, geographic refinement, and regional peculiarities may be crucial determinants of the results of studies on the relationship between fish assemblages and physical habitat of streams and therefore must be taken into account when comparing or applying such data (Mullen *et al*. 2011).

The present study contributed with novel evidence on the relevant physical habitat conditions for the conservation of stream fishes in the Neotropical region. Studies on the relationships between least-disturbed fauna and physical habitat of streams are commonly used by environmental protection agencies as reference standards for the efficient management in temperate regions (Karr 1991, Barbour *et al*. 1999, Bailey *et al*. 2014, Civas *et al*. 2016). But in the tropical regions studies on the subject are rare and mostly related to macroinvertebrates (Couceiro *et al*. 2012, Dedieu *et al*. 2015, Feio *et al*. 2015). Although macroinvertebrates are good indicators of water quality, the responses of the assemblages of other organisms to physical habitat conditions are equally important and may yield additional insights (Sullivan *et al*. 2008). Authors that worked with fish assemblages in tropical streams usually considered the indirect effects that various levels of human-induced physical habitat alterations had on those organisms (Casatti *et al*. 2006, Chakona & Swartz 2012, Kido *et al*. 2103, Terra *et al*. 2013, Teresa *et al*. 2015). The assessment of the consequences of human impacts on freshwater ecosystems is important but it is only effectively achieved when reference standards have been established (Hughes *et al*. 1998, Kershner *et al*. 2004, Kosnicki *et al*. 2014). Therefore, research on the natural relationships between animal assemblages and physical habitat conditions in pristine or least-disturbed sites is a basic step toward freshwater conservation. Some studies on tropical stream fishes focused on the influence of physical habitat on the structuring of fish assemblages in regions with little human interference but they were generally restricted to a small geographic area (Gerhard *et al*. 2004, Mendonça *et al*. 2005, Kano *et al*. 2013). Results for a small spatial scale are valuable for their refinement and local relevance but they usually ignore the importance of landscape influences on aquatic biota. That bias prevents the detection of landscape peculiarities and spatially constrains the applicability of the results. Our analyses of the influence of physical habitat conditions on fish assemblages of reference streams in the São Francisco river basin was the one over the largest spatial extent in the tropical region. Thus, our results are regionally remarkable for their relevance and potential management utility, and globally relevant for their contribution to the reduction of the gap of knowledge on the natural structuring of fish assemblages of tropical streams by physical habitat conditions.

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Supplementary Table 1 (S1). Number of individuals of the fish species sampled in refrenece streams of five national parks (PARNA) in the São Francisco river basin, Brazil. Parks were identified as follows: **CA -** PARNA Serra da Canastra; **CI -** PARNA Serra do Cipó; **CP -** PARNA Cavernas do Peruaçu; **SV -** PARNA Sempre-Vivas; **GS -** PARNA Grande Sertão Veredas.

Species	**CA**	**CI**	**CP**	**SV**	**GS**	**Total**
Astyanax cf *bockmanni*					4	**4**
Astyanax fasciatus	2	6	72		4	**84**
Astyanax lacustris					7	**7**
Astyanax rivularis	1550	686	109	675	67	**3087**
Astyanax sp A		23				**23**
Astyanax taeniatus		3				**3**
Bryconops sp					15	**15**
Centromochlus bockmanni					2	**2**
Cetopsorhamdia iheringi		3			10	**13**
Characidium cf *zebra*				1	41	**42**
Characidium fasciatum				5	2	**7**
Characidium sp B					2	**2**
Characidium sp A		1				**1**
Cichlasoma sanctifranciscense					1	**1**
Corydoras garbei					2	**2**
Eigenmannia gr. *trilineata*					16	**16**
Geophagus brasiliensis					1	**1**
Gymnotus aff *carapo*					4	**4**
Harttia longipinna		4				**4**
Harttia sp A	13					**13**
Harttia sp B	27	1				**28**
Harttia torrenticola	4					**4**
Hemigrammus marginatus					7	**7**
Hisonotus sp	12				173	**185**
Hisonotus sp B					3	**3**
Hoplias intermedius				3		**3**
Hyphessobrycon santae		7				**7**
Hypostomus francisci			1		3	**4**
Hypostomus lima			13	8	27	**48**

Imparfinis minutus					3	**3**
Knodus moenkhausii		4				**4**
Lepidocharax burnsi					1	**1**
Leporinus piau					1	**1**
Moenkhausia sanctaefilomenae					9	**9**
Neoplecostomus franciscoensis	2					**2**
Pareiorhina cepta	17					**17**
Phalloceros uai		275				**275**
Phenacogaster franciscoensis					33	**33**
Phenacorhamdia tenebrosa					4	**4**
Piabina argentea		2			15	**17**
Pimelodella lateristriga					3	**3**
Rhamdia aff *quelen*			20		7	**27**
Rineloricaria sp A					2	**2**
Serrapinus heterodon					19	**19**
Serrapinus piaba					14	**14**
Sternopygus macrurus					3	**3**
Synbranchus marmoratus					3	**3**
Trichomycterus brasiliensis	189	1	15	2		**207**
Trichomycterus sp A	3					**3**
Trichomycterus variegatus	29				1	**30**
Total	**1848**	**1016**	**230**	**694**	**509**	**4297**

Supplementary Table 2 (S2). Values for reference streams' physical-habitat metrics in five national parks (PARNA) in the São Francisco river basin, Brazil. Parks were identified as follows: **CA** - PARNA Serra da Canastra; **CI** - PARNA Serra do Cipó; **CP** - PARNA Cavernas do Peruaçu; **SV** - PARNA Sempre-Vivas; **GS** - PARNA Grande Sertão Veredas. Standard deviation and missing values are represented by 'SD' and 'NA', respectively.

Metrics	**CA**		**CI**		**CP**		**SV**		**GS**	
	Mean	(Min / Max)	Mean	(Min / Max)	Mean	(Min / Max)	Mean	(Min / Max)	Mean	(Min / Max)
Water chemistry										
Temperature (°C)	18.94	(10.59 / 22.54)	20.30	(18.00 / 24.21)	19.11	(19.11 / 19.11)	20.32	(17.09 / 22.29)	21.16	(19.67 / 22.14)
pH	5.68	(4.85 / 6.73)	NA	(NA / NA)	7.31	(7.31 / 7.31)	7.01	(6.39 / 7.55)	7.73	(7.11 / 7.92)
Conductivity 1 (μS/cm)	7.55	(2.40 / 14.6)	6.73	(2.22 / 17.93)	1038.00	(1038.00 / 1038.00)	0.62	(0.19 / 1.33)	0.21	(0.092 / 0.384)
Conductivity 2 (μS/cm)	6.88	(2.20 / 13.70)	4.16	(0 / 11.3)	921.00	(921.00 / 921.00)	467.63	(3.78 / 1251)	0.19	(0.084 / 0.359)
Dissolved oxygen (mg/L)	15.86	(5.13 / 86.00)	7.95	(6.94 / 8.46)	6.97	(6.97 / 6.97)	18.82	(5.39 / 78)	6.24	(4.85 / 7.86)
Dissolved oxygen (%)	72.26	(7.70 / 91.60)	88.61	(78 / 97.8)	75.60	(75.60 / 75.60)	66.65	(7.48 / 93.2)	69.78	(54.20 / 90.30)
Substrate										
Channel's and margins' substrate average immersion (%)	32.03	(23.82 / 41.63)	36.26	(14.73 / 70.36)	58.82	(58.82 / 58.82)	28.71	(3.64 / 42.09)	74.03	(11.67 / 95.09)
SD of channel's and margins' substrate average immersion (%)	29.78	(22.15 / 34.20)	28.43	(18.91 / 39.91)	44.14	(44.14 / 44.14)	35.15	(14.45 / 46.91)	26.86	(13.44 / 49.03)

Channel’s substrate average immersion (%)	31.13	(24.85 / 45.76)	35.89	(15.15 / 69.39)	56.06	(56.06 / 56.06)	26.19	(2.12 / 39.85)	76.91	(10.15 / 100.00)
SD of channel’s substrate average immersion (%)	27.33	(18.36 / 33.34)	28.26	(19.19 / 40.31)	45.08	(45.08 / 45.08)	32.23	(6.50 / 45.98)	23.13	(0.00 / 50.75)
Smooth bedrock (%)	11.85	(0.00 / 38.10)	6.80	(0.00 / 27.62)	0.00	(0.00 / 0.00)	5.44	(0.00 / 21.90)	0.12	(0.00 / 0.97)
Rugged bedrock (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	2.93	(0.00 / 7.77)	0.97	(0.00 / 7.77)
Bedrock (smooth + rugged) (%)	11.85	(0.00 / 38.10)	6.80	(0.00 / 27.62)	0.00	(0.00 / 0.00)	8.37	(2.86 / 22.86)	1.09	(0.00 / 8.74)
Large boulder (%)	5.50	(0.00 / 11.43)	13.71	(0.00 / 47.62)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	2.74	(0.00 / 17.14)
Small boulder (%)	24.34	(0.00 / 40.00)	26.85	(0.00 / 47.00)	0.00	(0.00 / 0.00)	7.85	(0.00 / 14.29)	0.00	(0.00 / 0.00)
Boulder (large + small) (%)	29.84	(0.00 / 51.43)	40.56	(0.00 / 71.43)	0.00	(0.00 / 0.00)	7.85	(0.00 / 14.29)	2.74	(0.00 / 17.14)
Cobble (%)	18.24	(5.71 / 39.05)	15.03	(0.00 / 33.33)	13.33	(13.33 / 13.33)	4.04	(0.00 / 20.39)	3.40	(0.00 / 27.18)
Coarse gravel (%)	9.44	(2.86 / 21.15)	9.44	(1.90 / 20.00)	0.95	(0.95 / 0.95)	4.22	(0.00 / 16.50)	0.97	(0.00 / 7.77)
Substrate > 16 mm diameter (%)	69.37	(47.62 / 89.52)	71.84	(3.00 / 97.00)	14.29	(14.29 / 14.29)	24.47	(7.29 / 41.75)	8.20	(0.00 / 43.69)
Fine gravel (%)	10.40	(0.95 / 25.00)	9.66	(0.00 / 20.00)	5.71	(5.71 / 5.71)	0.00	(0.00 / 0.00)	0.36	(0.00 / 2.91)
Sand (%)	5.40	(0 / 15.24)	10.31	(0.00 / 56.00)	1.90	(1.90 / 1.90)	10.57	(0.00 / 25.00)	4.84	(0.00 / 33.01)
Fine (%)	1.17	(0.00 / 5.77)	1.27	(0.00 / 7.00)	46.67	(46.67 / 46.67)	4.85	(0.00 / 24.27)	23.34	(0.00 / 92.38)
Substrate < 16 mm diameter (%)	16.96	(2.86 / 30.77)	21.24	(0.00 / 83.00)	54.29	(54.29 / 54.29)	15.43	(1.90 / 26.04)	28.55	(0.00 / 92.38)

Total organic (%)	10.49	(2.86 / 32.38)	6.78	(0.00 / 14.00)	5.71	(5.71 / 5.71)	117.12	(100.95 / 131.25)	54.92	(0.95 / 97.14)
Wood (%)	0.00	(0.00 / 0.00)	0.85	(0.00 / 5.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	1.94	(0.00 / 15.53)
Concrete (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	2.93	(0.00 / 7.77)	0.97	(0.00 / 7.77)
Hard pan (%)	0.85	(0.00 / 5.77)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.83	(0.00 / 6.67)
Other (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.95	(0.00 / 4.76)	0.00	(0.00 / 0.00)
Roots (%)	2.12	(0.00 / 7.62)	1.50	(0.00 / 4.76)	0.00	(0.00 / 0.00)	0.32	(0.00 / 1.94)	45.36	(0.00 / 87.62)
Fine litter (%)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	100.00	(100.00 / 100.00)	3.93	(0.00 / 10.48)
Coarse litter (%)	8.16	(0.00 / 28.57)	3.75	(0.00 / 8.00)	5.71	(5.71 / 5.71)	11.10	(0.95 / 28.13)	3.69	(0.00 / 16.19)
Filamentous algae (%)	0.21	(0.00 / 1.90)	0.68	(0.00 / 3.81)	0.00	(0.00 / 0.00)	5.70	(0.00 / 18.45)	0.00	(0.00 / 0.00)
Aquatic macrophyte (%)	0.74	(0.00 / 3.81)	0.14	(0.00 / 0.95)	0.95	(0.95 / 0.95)	23.33	(0.00 / 62.86)	0.12	(0.00 / 0.95)
Small sediment on channel bed (%)	0.08	(0.00 / 0.24)	0.11	(0.00 / 0.67)	0.67	(0.67 / 0.67)	0.10	(0.00 / 0.21)	0.84	(0.06 / 1.00)
Mean substrate size	0.25	(0.16 / 0.30)	0.20	(-0.03 / 0.29)	-0.11	(-0.11 / -0.11)	0.25	(0.07 / 0.39)	-0.07	(-0.26 / 0.24)
Filamentous algae + aquatic macrophyte (%)	0.95	(0.00 / 4.76)	0.82	(0.00 / 4.76)	0.95	(0.95 / 0.95)	29.03	(3.13 / 62.86)	0.12	(0.00 / 0.95)
Roots + fine litter + coarse litter (%)	10.27	(2.86 / 32.38)	5.25	(0.00 / 11.43)	5.71	(5.71 / 5.71)	111.42	(100.95 / 128.13)	52.98	(0.00 / 97.14)
Sand + fine (%)	6.57	(0.00 / 15.24)	11.59	(0.00 / 63.00)	48.57	(48.57 / 48.57)	15.43	(1.90 / 26.04)	28.19	(0.00 / 92.38)

Log10 [estimated geometric mean substrate diameter (mm)]	2.04	(1.19 / 2.57)	2.00	(-0.24 / 2.73)	-0.69	(-0.69 / -0.69)	-22.06	(-109.54 / -0.29)	-0.48	(-1.91 / 0.93)
Log10 [relative bed stability]	1.31	(-0.43 / 2.81)	1.57	(-1.58 / 2.69)	-0.93	(-0.93 / -0.93)	-22.34	(-109.30 / -0.67)	-0.82	(-2.75 / 0.68)
Relative bed stability	0.72	(-0.39 / 1.61)	0.43	(-0.21 / 1.34)	0.24	(0.24 / 0.24)	0.28	(-0.23 / 0.71)	0.35	(-0.28 / 0.85)
Deviation of substrate diameter	0.40	(0.26 / 0.54)	0.35	(0.14 / 0.53)	0.55	(0.55 / 0.55)	0.58	(0.31 / 0.98)	0.33	(0.15 / 0.75)
Fish shelter										
Filamentous algae areal cover	1.19	(0.00 / 8.41)	37.37	(0.00 / 84.77)	0.00	(0.00 / 0.00)	9.09	(0.00 / 33.41)	0.00	(0.00 / 0.00)
Aquatic macrophyte areal cover	8.84	(0.00 / 39.55)	10.65	(0.00 / 42.95)	0.00	(0.00 / 0.00)	22.65	(0.00 / 55.91)	5.82	(0.00 / 25.91)
Large woody debris areal cover	1.39	(0.00 / 10.23)	1.56	(0.00 / 9.55)	0.00	(0.00 / 0.00)	0.45	(0.00 / 1.82)	2.78	(0.00 / 5.45)
Brush and small woody debris areal cover	22.98	(0.00 / 57.05)	7.31	(0.00 / 26.82)	23.18	(23.18 / 23.18)	5.15	(1.82 / 19.09)	46.79	(0.00 / 87.50)
Root areal cover	6.74	(0.00 / 17.73)	22.60	(5.68 / 70.91)	43.86	(43.86 / 43.86)	11.17	(4.55 / 23.41)	37.27	(0.00 / 84.77)
Leaf bank areal cover	54.32	(0.45 / 87.50)	35.26	(0.00 / 82.05)	22.95	(22.95 / 22.95)	25.19	(0.00 / 71.14)	37.64	(0.00 / 84.77)
Overhanging vegetation areal cover	11.64	(0.45 / 34.77)	16.79	(5.45 / 48.64)	21.59	(21.59 / 21.59)	26.82	(1.36 / 57.27)	32.98	(6.82 / 87.50)
Undercut bank areal cover	9.04	(0.00 / 25.00)	16.95	(0.00 / 40.00)	0.00	(0.00 / 0.00)	2.42	(0.00 / 5.45)	8.27	(0.00 / 41.82)
Boulder areal cover	67.98	(3.64 / 87.50)	66.53	(0.00 / 87.50)	0.91	(0.91 / 0.91)	48.33	(4.55 / 87.50)	11.22	(0.00 / 87.50)
Artificial structure areal cover	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)

Total areal cover for fish except filamentous algae and aquatic macrophytes	174.09	(96.82 / 250.23)	166.98	(105.91 / 288.64)	112.50	(112.50 / 112.50)	119.55	(41.82 / 188.64)	176.96	(80.00 / 370.23)
Total areal cover for fish	184.12	(107.50 / 250.23)	215.00	(133.18 / 352.50)	112.50	(112.50 / 112.50)	151.29	(107.05 / 200.68)	182.78	(80.00 / 370.23)
Total areal cover of large wood, brush, overhanging vegetation, boulders, and undercut banks	113.03	(90.23 / 145.45)	109.12	(72.05 / 140.91)	45.68	(45.68 / 45.68)	83.18	(30.68 / 141.14)	102.05	(53.64 / 220.00)
Total areal cover of large wood, brush, overhanging vegetation, boulders, undercut banks, leaf banks, and roots	174.09	(96.82 / 250.23)	166.98	(105.91 / 288.64)	112.50	(112.50 / 112.50)	119.55	(41.82 / 188.64)	176.96	(80.00 / 370.23)
Anthropogenic structures areal cover	10.03	(0.00 / 47.95)	48.02	(0.00 / 127.73)	0.00	(0.00 / 0.00)	31.74	(0.00 / 89.32)	5.82	(0.00 / 25.91)
Total areal cover of large wood, boulders, undercut banks, and human structures	78.41	(19.55 / 100.45)	85.03	(39.77 / 100.68)	0.91	(0.91 / 0.91)	51.21	(5.91 / 89.32)	22.27	(0.00 / 88.41)
Filamentous algae and aquatic macrophyte areal cover	10.03	(0.00 / 47.95)	48.02	(0.00 / 127.73)	0.00	(0.00 / 0.00)	31.74	(0.00 / 89.32)	5.82	(0.00 / 25.91)
Large and small woody debris areal cover	24.37	(0.00 / 57.05)	8.86	(0.00 / 36.36)	23.18	(23.18 / 23.18)	5.61	(1.82 / 20.91)	49.57	(0.00 / 90.68)
Roots and overhanging vegetation areal cover	18.38	(0.91 / 45.23)	39.38	(13.18 / 89.32)	65.45	(65.45 / 65.45)	37.99	(5.91 / 75.45)	70.26	(12.50 / 172.27)
Proportion of reach with filamentous algae cover	0.03	(0.00 / 0.18)	0.77	(0.00 / 1.00)	0.00	(0.00 / 0.00)	0.33	(0.00 / 0.91)	0.00	(0.00 / 0.00)
Proportion of reach with aquatic macrophyte cover	0.17	(0.00 / 0.55)	0.29	(0.00 / 0.73)	0.00	(0.00 / 0.00)	0.79	(0.00 / 1.00)	0.18	(0.00 / 0.91)
Proportion of reach with large woody debris cover	0.09	(0.00 / 0.36)	0.16	(0.00 / 0.82)	0.00	(0.00 / 0.00)	0.09	(0.00 / 0.36)	0.28	(0.00 / 0.55)
Proportion of reach with small woody debris cover	0.54	(0.00 / 1.00)	0.36	(0.00 / 0.91)	0.91	(0.91 / 0.91)	0.44	(0.36 / 0.64)	0.81	(0.00 / 1.00)

Proportion of reach with root cover	0.24	(0.00 / 0.55)	0.55	(0.18 / 1.00)	1.00	(1.00 / 1.00)	0.71	(0.36 / 1.00)	0.63	(0.00 / 1.00)
Proportion of reach with leaf bank cover	0.87	(0.09 / 1.00)	0.77	(0.00 / 1.00)	1.00	(1.00 / 1.00)	0.56	(0.00 / 1.00)	0.74	(0.00 / 1.00)
Proportion of reach with overhanging vegetation cover	0.44	(0.09 / 0.91)	0.69	(0.18 / 0.91)	0.91	(0.91 / 0.91)	0.83	(0.27 / 1.00)	0.91	(0.64 / 1.00)
Proportion of reach with undercut bank cover	0.35	(0.00 / 0.91)	0.44	(0.00 / 1.00)	0.00	(0.00 / 0.00)	0.24	(0.00 / 0.55)	0.30	(0.00 / 1.00)
Proportion of reach with boulder cover	0.92	(0.36 / 1.00)	0.79	(0.00 / 1.00)	0.18	(0.18 / 0.18)	0.85	(0.55 / 1.00)	0.14	(0.00 / 1.00)
Proportion of reach with artificial structure cover	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Proportion of reach with any cover except filamentous algae and aquatic macrophyte	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with any cover	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with large wood, brush, overhanging vegetation, boulders, or undercut banks cover	1.00	(1.00 / 1.00)	0.99	(0.91 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with large wood, brush, overhanging vegetation, boulders, undercut banks, leaf banks, or roots cover	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with anthropogenic structures	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Proportion of reach with large wood, boulders, undercut banks, or human structures cover	0.18	(0.00 / 0.64)	0.81	(0.00 / 1.00)	0.00	(0.00 / 0.00)	0.79	(0.00 / 1.00)	0.18	(0.00 / 0.91)

Riparian vegetation

Mean canopy density mid-stream (%)	71.51	(12.43 / 99.87)	60.39	(17.11 / 99.73)	94.79	(94.79 / 94.79)	38.86	(5.88 / 83.42)	82.62	(37.30 / 100.00)
SD of mean canopy density mid-stream (%)	16.65	(0.44 / 36.83)	24.17	(0.59 / 42.31)	2.66	(2.66 / 2.66)	28.39	(15.35 / 40.63)	8.15	(0.00 / 24.65)
Mean canopy density at bank (%)	80.60	(24.33 / 99.47)	76.32	(51.34 / 99.73)	97.33	(97.33 / 97.33)	52.99	(22.19 / 91.98)	91.34	(50.80 / 100.00)
SD of mean canopy density at bank (%)	13.91	(1.77 / 35.45)	21.57	(0.89 / 40.32)	3.34	(3.34 / 3.34)	26.54	(9.12 / 37.06)	7.45	(0.00 / 26.38)
Riparian canopy (> 5 m high) cover - trees > 0.3 m DBH	3.61	(0.00 / 6.82)	3.15	(0.23 / 12.05)	5.00	(5.00 / 5.00)	1.89	(0.23 / 4.55)	4.35	(0.68 / 11.02)
SD of riparian canopy (> 5 m high) cover - trees > 0.3 m DBH	4.43	(0.00 / 9.26)	3.17	(0.75 / 5.93)	6.02	(6.02 / 6.02)	2.31	(0.75 / 4.40)	6.19	(1.17 / 16.80)
Riparian canopy (> 5 m high) cover - trees < 0.3 m DBH	26.70	(0.00 / 63.86)	14.81	(4.55 / 40.80)	22.39	(22.39 / 22.39)	16.21	(1.82 / 36.82)	47.22	(9.77 / 84.77)
SD of riparian canopy (> 5 m high) cover - trees < 0.3 m DBH	14.56	(0.00 / 20.43)	14.37	(5.90 / 34.75)	13.21	(13.21 / 13.21)	10.45	(1.17 / 17.30)	18.39	(9.05 / 37.44)
Riparian mid-layer (0.5 to 5 m high) woody cover	15.49	(3.75 / 31.14)	13.96	(2.50 / 25.23)	55.68	(55.68 / 55.68)	24.47	(4.09 / 41.70)	20.63	(0.00 / 60.80)
SD of riparian mid-layer (0.5 to 5 m high) woody cover	17.03	(9.10 / 24.11)	10.96	(5.00 / 18.08)	25.43	(25.43 / 25.43)	12.03	(6.88 / 20.99)	15.53	(0.00 / 29.96)
Riparian mid-layer (0.5 to 5 m high) herbaceous cover	9.85	(0.00 / 27.16)	12.53	(5.23 / 27.95)	20.23	(20.23 / 20.23)	6.06	(0.45 / 10.91)	49.90	(0.00 / 87.50)
SD of riparian mid-layer (0.5 to 5 m high) herbaceous cover	12.95	(0.00 / 29.72)	12.08	(5.03 / 17.66)	21.28	(21.28 / 21.28)	4.67	(1.01 / 10.37)	19.85	(0.00 / 37.26)
Riparian ground-layer (< 0.5 m high) woody cover	7.13	(0.23 / 39.55)	28.18	(18.52 / 41.70)	9.55	(9.55 / 9.55)	7.22	(0.00 / 13.30)	13.59	(1.36 / 40.91)

SD of riparian ground-layer (< 0.5 m high) woody cover	8.41	(0.75 / 29.31)	21.51	(13.53 / 30.90)	19.73	(19.73 / 19.73)	6.62	(0.00 / 12.02)	16.79	(4.52 / 38.15)
Riparian ground-layer (< 0.5 m high) herbaceous cover	39.63	(2.61 / 65.11)	33.96	(17.84 / 56.02)	25.45	(25.45 / 25.45)	27.48	(4.09 / 58.98)	46.45	(21.93 / 87.50)
SD of riparian ground-layer (< 0.5 m high) herbaceous cover	23.15	(8.67 / 32.78)	19.42	(11.47 / 27.23)	25.21	(25.21 / 25.21)	15.08	(5.51 / 29.93)	16.94	(0.00 / 30.76)
Riparian ground-layer (< 0.5 m high) bare ground cover	26.41	(0.00 / 79.55)	15.89	(0.23 / 43.52)	0.00	(0.00 / 0.00)	35.23	(11.36 / 56.02)	10.65	(0.00 / 52.27)
SD of riparian ground-layer (< 0.5 m high) bare ground cover	15.56	(0.00 / 32.19)	14.27	(0.75 / 25.28)	0.00	(0.00 / 0.00)	19.30	(10.73 / 31.42)	5.00	(0.00 / 21.00)
Riparian canopy cover (XCL + XCS)	30.32	(0.00 / 70.57)	17.95	(4.77 / 45.11)	27.39	(27.39 / 27.39)	18.11	(2.05 / 41.36)	51.56	(20.80 / 87.84)
SD of riparian canopy cover (XCL + XCS)	15.68	(0.00 / 22.36)	16.02	(6.27 / 38.94)	17.07	(17.07 / 17.07)	10.70	(1.51 / 17.43)	19.02	(8.59 / 37.57)
Riparian mid-layer cover (XMW + XMH)	25.34	(7.05 / 51.14)	26.49	(10.23 / 49.43)	75.91	(75.91 / 75.91)	30.53	(4.77 / 49.20)	70.53	(22.95 / 148.30)
SD of riparian mid-layer cover (XMW + XMH)	21.21	(10.79 / 37.54)	17.86	(8.70 / 30.07)	30.12	(30.12 / 30.12)	12.97	(7.94 / 22.97)	28.16	(20.17 / 37.85)
Riparian ground-layer vegetation cover (XGW + XGH)	46.77	(3.75 / 101.48)	62.14	(36.36 / 97.73)	35.00	(35.00 / 35.00)	34.70	(4.09 / 65.80)	60.04	(23.30 / 124.32)
SD odf riparian ground-layer vegetation cover (XGW + XGH)	26.25	(9.10 / 38.86)	34.88	(22.09 / 52.41)	31.63	(31.63 / 31.63)	16.88	(5.51 / 25.44)	26.74	(16.86 / 41.41)
Riparian canopy + mid-layer cover (XC + XM)	55.66	(17.16 / 83.75)	44.45	(15.00 / 65.68)	103.30	(103.30 / 103.30)	48.64	(22.61 / 79.20)	122.09	(43.75 / 196.36)
SD of riparian canopy + mid-layer cover (XC + XM)	26.24	(15.05 / 50.37)	26.42	(13.70 / 48.90)	32.09	(32.09 / 32.09)	18.28	(8.44 / 28.49)	35.20	(24.71 / 52.30)

Riparian canopy + mid-layer woody cover (XC + XM)	45.81	(9.55 / 78.30)	31.92	(7.27 / 50.80)	83.07	(83.07 / 83.07)	42.58	(21.93 / 68.30)	72.19	(33.07 / 120.91)
SD of riparian canopy + mid-layer woody cover (XC + XM)	23.01	(15.05 / 37.51)	20.55	(6.66 / 37.93)	23.13	(23.13 / 23.13)	17.27	(7.25 / 27.35)	21.74	(8.59 / 35.23)
Riparian cover, sum of 3 layers (XC + XM + XG)	102.42	(78.41 / 124.20)	106.59	(76.36 / 163.41)	138.30	(138.30 / 138.30)	83.33	(26.70 / 124.77)	182.13	(121.82 / 320.68)
SD of riparian cover, sum of 3 layers (XC + XM + XG)	28.00	(15.17 / 45.00)	33.99	(22.91 / 44.96)	33.82	(33.82 / 33.82)	25.07	(12.65 / 37.67)	32.10	(19.70 / 50.52)
Riparian woody cover, sum of 3 layers (XC + XMW + XGW)	52.94	(25.68 / 79.43)	60.10	(37.50 / 79.66)	92.61	(92.61 / 92.61)	49.79	(21.93 / 81.14)	85.78	(40.11 / 149.77)
SD of riparian woody cover, sum of 3 layers (XC + XMW + XGW)	24.28	(12.23 / 34.50)	24.76	(14.65 / 41.83)	34.85	(34.85 / 34.85)	18.86	(8.02 / 29.82)	22.24	(4.16 / 35.03)
Riparian canopy presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Riparian mid-layer presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Riparian ground cover presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Riparian canopy and mid-layer presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
3-layer riparian vegetation presence (proportion of reach)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)	1.00	(1.00 / 1.00)
Large wood debris in active channel (pieces/100 m) - size class 1	4.89	(0.00 / 17.33)	8.86	(0.00 / 50.67)	17.33	(17.33 / 17.33)	1.00	(0.00 / 4.00)	16.33	(0.67 / 30.67)
Large wood debris in active channel (pieces/100 m) - size class 2	1.11	(0.00 / 5.33)	1.81	(0.00 / 10.00)	1.33	(1.33 / 1.33)	0.00	(0.00 / 0.00)	3.58	(0.00 / 10.67)

Large wood debris in active channel (pieces/100 m) - size class 3	0.00	(0.00 / 0.00)	0.67	(0.00 / 3.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.17	(0.00 / 0.67)
Large wood debris in active channel (pieces/100 m) - size class 4	0.00	(0.00 / 0.00)	0.19	(0.00 / 1.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/100 m) - size class 1	0.63	(0.00 / 2.87)	2.38	(0.00 / 14.41)	1.37	(1.37 / 1.37)	0.06	(0.00 / 0.23)	2.19	(0.04 / 5.18)
Large wood debris volume in active channel (m^3/100 m) - size class 2	0.00	(0.00 / 0.00)	1.63	(0.00 / 10.03)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.17	(0.00 / 0.69)
Large wood debris volume in active channel (m^3/100 m) - size class 3	0.41	(0.00 / 2.18)	1.97	(0.00 / 12.05)	0.44	(0.44 / 0.44)	0.00	(0.00 / 0.00)	1.45	(0.00 / 4.02)
Large wood debris volume in active channel (m^3/100 m) - size class 4	0.00	(0.00 / 0.00)	1.14	(0.00 / 7.95)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/100 m) - size class 1	2.30	(0.00 / 8.67)	5.81	(0.00 / 32.00)	6.67	(6.67 / 6.67)	1.11	(0.00 / 3.33)	4.33	(0.00 / 8.00)
Large wood debris above active channel (pieces/100 m) - size class 2	0.81	(0.00 / 4.00)	1.24	(0.00 / 7.33)	3.33	(3.33 / 3.33)	0.44	(0.00 / 2.00)	0.75	(0.00 / 2.67)
Large wood debris above active channel (pieces/100 m) - size class 3	0.30	(0.00 / 1.33)	0.57	(0.00 / 4.00)	0.67	(0.67 / 0.67)	0.11	(0.00 / 0.67)	0.08	(0.00 / 0.67)
Large wood debris above active channel (pieces/100 m) - size class 4	0.15	(0.00 / 1.33)	0.19	(0.00 / 1.33)	0.00	(0.00 / 0.00)	0.11	(0.00 / 0.67)	0.00	(0.00 / 0.00)

Large wood debris above active channel (pieces/100 m) - size class 5	**0.00**	**(0.00 / 0.00)**	**0.00**	**(0.00 / 0.00)**	**0.00**	**(0.00 / 0.00)**	**0.00**	**(0.00 / 0.00)**	**0.00**	**(0.00 / 0.00)**
Large wood debris volume above active channel (m^3/100 m) - size class 1	1.89	(0.00 / 14.34)	2.20	(0.00 / 14.66)	1.78	(1.78 / 1.78)	0.38	(0.00 / 1.99)	0.50	(0.00 / 1.49)
Large wood debris volume above active channel (m^3/100 m) - size class 2	1.80	(0.00 / 14.15)	1.94	(0.00 / 13.22)	1.58	(1.58 / 1.58)	0.34	(0.00 / 1.91)	0.30	(0.00 / 1.26)
Large wood debris volume above active channel (m^3/100 m) - size class 3	1.55	(0.00 / 12.56)	1.76	(0.00 / 12.32)	0.69	(0.69 / 0.69)	0.28	(0.00 / 1.67)	0.09	(0.00 / 0.69)
Large wood debris volume above active channel (m^3/100 m) - size class 4	1.40	(0.00 / 12.56)	1.17	(0.00 / 8.22)	0.00	(0.00 / 0.00)	0.28	(0.00 / 1.67)	0.00	(0.00 / 0.00)
Large wood debris volume above active channel (m^3/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/100 m) - size class 1	7.19	(0.00 / 19.33)	14.67	(0.00 / 82.67)	24.00	(24.00 / 24.00)	2.11	(0.00 / 6.67)	20.67	(1.33 / 34.00)
Large wood debris in and above active channel (pieces/100 m) - size class 2	1.93	(0.00 / 6.67)	3.05	(0.00 / 17.33)	4.67	(4.67 / 4.67)	0.44	(0.00 / 2.00)	4.33	(0.00 / 10.67)
Large wood debris in and above active channel (pieces/100 m) - size class 3	0.30	(0.00 / 1.33)	1.24	(0.00 / 7.33)	0.67	(0.67 / 0.67)	0.11	(0.00 / 0.67)	0.25	(0.00 / 1.33)
Large wood debris in and above active channel (pieces/100 m) - size class 4	0.15	(0.00 / 1.33)	0.38	(0.00 / 2.67)	0.00	(0.00 / 0.00)	0.11	(0.00 / 0.67)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/100 m) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)

Large wood debris volume in and above active channel (m^3/100 m) - size class 1	2.52	(0.00 / 15.47)	4.58	(0.00 / 29.06)	3.15	(3.15 / 3.15)	0.44	(0.00 / 1.99)	2.69	(0.08 / 5.30)
Large wood debris volume in and above active channel (m^3/100 m) - size class 2	2.21	(0.00 / 15.23)	3.91	(0.00 / 25.28)	2.03	(2.03 / 2.03)	0.34	(0.00 / 1.91)	1.74	(0.00 / 4.03)
Large wood debris volume in and above active channel (m^3/100 m) - size class 3	1.55	(0.00 / 12.56)	3.39	(0.00 / 22.35)	0.69	(0.69 / 0.69)	0.28	(0.00 / 1.67)	0.26	(0.00 / 1.39)
Large wood debris volume in and above active channel (m^3/100 m) - size class 4	1.40	(0.00 / 12.56)	2.31	(0.00 / 16.17)	0.00	(0.00 / 0.00)	0.28	(0.00 / 1.67)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/100 m) - size class 5	0.00	(0.00 /0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/m^2) - size class 1	0.01	(0.00 / 0.03)	0.01	(0.00 / 0.08)	0.09	(0.09 / 0.09)	0.00	(0.00 / 0.00)	0.06	(0.00 / 0.10)
Large wood debris in active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.02)
Large wood debris in active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/m^2) - size class 1	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.01)

Large wood debris volume in active channel (m^3/m^2) - size class 2	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)
Large wood debris volume in active channel (m^3/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in active channel (m^3/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 1	0.01	(0.00 / 0.02)	0.01	(0.00 / 0.05)	0.03	(0.03 / 0.03)	0.00	(0.00 / 0.00)	0.02	(0.00 / 0.03)
Large wood debris above active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.01)	0.02	(0.02 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)
Large wood debris above active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 1	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.02)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.02)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)

Large wood debris above active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris above active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/m^2) - size class 1	0.02	(0.00 / 0.04)	0.02	(0.00 / 0.13)	0.12	(0.12 / 0.12)	0.00	(0.00 / 0.01)	0.08	(0.00 / 0.12)
Large wood debris in and above active channel (pieces/m^2) - size class 2	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.03)	0.02	(0.02 / 0.02)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.03)
Large wood debris in and above active channel (pieces/m^2) - size class 3	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/m^2) - size class 4	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris in and above active channel (pieces/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/m^2) - size class 1	0.01	(0.00 / 0.03)	0.01	(0.00 / 0.05)	0.02	(0.02 / 0.02)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.02)
Large wood debris volume in and above active channel (m^3/m^2) - size class 2	0.00	(0.00 / 0.03)	0.01	(0.00 / 0.04)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.01)
Large wood debris volume in and above active channel (m^3/m^2) - size class 3	0.00	(0.00 / 0.03)	0.01	(0.00 / 0.04)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Large wood debris volume in and above active channel (m^3/m^2) - size class 4	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.03)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)

Large wood debris volume in and above active channel (m^3/m^2) - size class 5	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Small wood debris volume in active channel (m^3/m^2)	0.00	(0.00 / 0.01)	0.00	(0.00 / 0.01)	0.01	(0.01 / 0.01)	0.00	(0.00 / 0.00)	0.01	(0.00 / 0.01)
Small wood debris volume above active channel (m^3/m^2)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Small wood debris volume in active channel (m^3/100 m)	0.63	(0.00 / 2.87)	0.75	(0.00 / 4.38)	1.37	(1.37 / 1.37)	0.06	(0.00 / 0.23)	2.01	(0.04 / 4.49)
Small wood debris volume above active channel (m^3/100 m)	0.09	(0.00 / 0.43)	0.27	(0.00 / 1.43)	0.19	(0.19 / 0.19)	0.04	(0.00 / 0.15)	0.21	(0.00 / 0.46)
Channel morphology										
Water flow (m^3/s)	0.12	(0.00 / 0.36)	0.13	(0.00 / 0.45)	0.08	(0.08 / 0.08)	0.16	(0.01 / 0.37)	0.40	(0.05 / 1.05)
Water flow corrected for type of channel bed (m^3/s)	0.10	(0.00 / 0.28)	0.11	(0.00 / 0.36)	0.07	(0.07 / 0.07)	0.13	(0.01 / 0.30)	0.34	(0.05 / 0.84)
Mean water velocity (m/s)	0.02	(0.01 / 0.03)	0.10	(0.06 / 0.16)	0.37	(0.37 / 0.37)	0.54	(0.04 / 2.22)	0.85	(0.17 / 2.17)
SD of mean water velocity (m/s)	0.02	(0.00 / 0.05)	0.08	(0.04 / 0.16)	0.40	(0.40 / 0.40)	0.78	(0.01 / 3.43)	0.32	(0.06 / 1.10)
Depth ratio of bankfull thalweg / thalweg	3.52	(1.69 / 6.30)	3.83	(2.52 / 7.02)	1.91	(1.91 / 1.91)	3.12	(1.96 / 3.86)	2.54	(1.08 / 6.30)
Mean depth of bankfull thalweg (thalweg + bankfull channel height) (m)	1.20	(0.79 / 1.84)	1.19	(0.72 / 1.84)	0.60	(0.60 / 0.60)	1.04	(0.82 / 1.32)	1.40	(0.59 / 3.03)
Ratio bankfull width / bankfull thalweg depth	4.01	(2.66 / 5.62)	6.77	(2.97 / 11.50)	3.24	(3.24 / 3.24)	8.49	(5.10 / 10.50)	2.74	(0.00 / 5.35)

Mean thalweg depth - section (cm)	29.49	(14.58 / 54.95)	23.79	(14.98 / 34.40)	29.02	(29.02 / 29.02)	25.25	(12.60 / 47.11)	48.28	(24.56 / 89.27)
SD of mean thalweg depth - section (cm)	20.98	(11.49/ 33.64)	14.82	(8.74 / 22.13)	22.60	(22.60 / 22.60)	20.71	(9.94 / 32.98)	22.25	(15.10 / 31.52)
Mean thalweg depth (cm)	36.86	(20.28 / 53.45)	32.14	(23.39 / 37.99)	31.45	(31.45 / 31.45)	35.79	(21.30 / 63.12)	62.27	(35.38 / 94.94)
SD of mean thalweg depth (cm)	23.37	(13.39 / 32.19)	16.31	(8.93 / 19.90)	17.93	(17.93 / 17.93)	19.86	(14.80 / 31.85)	18.82	(12.13 / 22.39)
Mean wetted width (m)	3.10	(2.13 / 4.66)	3.52	(2.44 / 4.33)	1.53	(1.53 / 1.53)	3.00	(1.95 / 4.55)	3.12	(0.71 / 10.30)
SD of mean wetted width (m)	1.68	(0.89 / 3.22)	1.67	(0.69 / 2.41)	0.47	(0.47 / 0.47)	1.31	(0.86 / 1.84)	1.12	(0.13 / 5.50)
Mean channel bar width (m)	0.17	(0.00 / 0.65)	0.11	(0.00 / 0.28)	0.00	(0.00 / 0.00)	0.40	(0.23 / 0.70)	0.35	(0.00 / 2.75)
Mean bankfull wetted width (m)	4.61	(2.78 / 5.69)	7.18	(3.89 / 11.21)	1.95	(1.95 / 1.95)	8.54	(6.33 / 9.41)	4.54	(0.00 / 16.20)
SD of mean bankfull wetted width (m)	1.90	(0.63 / 3.56)	1.95	(0.91 / 4.08)	0.45	(0.45 / 0.45)	3.85	(2.21 / 4.98)	1.26	(0.00 / 3.56)
Mean bankfull channel height (m)	0.83	(0.37 / 1.55)	0.87	(0.49 / 1.58)	0.29	(0.29 / 0.29)	0.68	(0.61 / 0.91)	0.77	(0.05 / 2.55)
SD of mean bankfull channel height (m)	0.38	(0.11 / 1.72)	0.54	(0.02 / 1.84)	0.14	(0.14 / 0.14)	0.20	(0.16 / 0.27)	0.32	(0.05 / 1.10)
Mean wetted width x depth - section (m^2)	1.11	(0.31 / 2.25)	0.92	(0.47 / 1.68)	0.51	(0.51 / 0.51)	0.87	(0.29 / 1.48)	1.46	(0.22 / 4.32)
SD of mean wetted width x depth - section (m^2)	1.11	(0.21 / 2.23)	0.79	(0.31 / 1.75)	0.44	(0.44 / 0.44)	0.66	(0.35 / 0.90)	0.60	(0.05 / 2.29)
Mean wetted width / depth - section (m/m)	0.11	(0.07 / 0.22)	0.09	(0.04 / 0.14)	0.17	(0.17 / 0.17)	0.10	(0.06 / 0.16)	0.28	(0.07 / 0.49)
SD of mean wetted width / depth - section (m/m)	0.08	(0.03 / 0.15)	0.07	(0.03 / 0.22)	0.11	(0.11 / 0.11)	0.06	(0.03 / 0.15)	0.13	(0.04 / 0.24)

Mean wetted width x depth (m^2)	1.19	(0.43 / 2.44)	1.15	(0.58 / 1.64)	0.48	(0.48 / 0.48)	1.13	(0.41 / 1.85)	1.86	(0.38 / 4.95)
Mean wetted width / depth (m/m)	8.70	(4.68 / 10.89)	11.08	(7.69 / 16.25)	4.87	(4.87 / 4.87)	8.85	(4.52 / 12.78)	5.71	(1.30 / 21.44)
Mean bank angle (degrees)	41.36	(28.82 / 57.36)	30.99	(28.05 / 36.00)	34.55	(34.55 / 34.55)	34.70	(27.82 / 50.68)	38.75	(0.00 / 62.95)
SD of mean bank angle (degrees)	18.88	(16.16 / 22.07)	14.51	(9.25 / 19.67)	13.88	(13.88 / 13.88)	15.64	(8.86 / 18.55)	12.30	(0.00 / 21.30)
Mean bank undercut distance (m)	0.02	(0.00 / 0.09)	0.02	(0.00 / 0.05)	0.00	(0.00 / 0.00)	0.02	(0.00 / 0.06)	0.02	(0.00 / 0.12)
SD of mean bank undercut distance (m)	0.05	(0.00 / 0.14)	0.06	(0.00 / 0.19)	0.00	(0.00 / 0.00)	0.08	(0.00 / 0.16)	0.05	(0.00 / 0.31)
Mean residual pool depth (m^2/100 m of reach)	26.44	(13.05 / 45.85)	20.10	(11.98 / 26.37)	24.55	(24.55 / 24.55)	25.88	(18.36 / 49.26)	29.13	(19.68 / 48.28)
Mean residual pool depth (m^2/100 m of reach) / Mean thalweg depth (cm)	0.71	(0.61 / 0.88)	0.62	(0.51 / 0.69)	0.78	(0.78 / 0.78)	0.73	(0.60 / 0.86)	0.48	(0.35 / 0.72)
Percent falls	4.52	(0.00 / 19.33)	2.67	(0.00 / 6.00)	0.67	(0.67 / 0.67)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)
Percent cascade	0.07	(0.00 / 0.67)	0.00	(0.00 / 0.00)	0.67	(0.67 / 0.67)	3.78	(0.00 / 11.33)	2.25	(0.00 / 17.33)
Percent rapids	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	5.67	(0.00 / 31.33)
Percent riffle	39.41	(9.33 / 59.33)	38.76	(21.33 / 58.67)	35.33	(35.33 / 35.33)	0.00	(0.00 / 0.00)	71.92	(14.00 / 100.00)
Percent glide	45.85	(20.67 / 74.67)	56.38	(26.00 / 78.00)	63.33	(63.33 / 63.33)	1.67	(0.00 / 10.00)	18.92	(0.00 / 66.00)
Percent impoundment pool	0.89	(0.00 / 8.00)	1.43	(0.00 / 10.00)	0.00	(0.00 / 0.00)	5.11	(0.00 / 12.00)	0.00	(0.00 / 0.00)
Percent plunge pool	1.70	(0.00 / 15.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	25.78	(2.00 / 44.67)	0.00	(0.00 / 0.00)

Percent lateral scour pool	1.78	(0.00 / 9.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	100.00	(100.00 / 100.00)	0.33	(0.00 / 2.67)
Percent trench pool	5.78	(0.00 / 52.00)	0.76	(0.00 / 5.33)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.25	(0.00 / 2.00)
Percent bcakwater pool	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	5.78	(0.00 / 21.33)	0.67	(0.00 / 5.33)
Percent dry channel	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	0.00	(0.00 / 0.00)	57.89	(32.00 / 98.00)	0.00	(0.00 / 0.00)
Percent falls + cascade + rapids + riffles	44.00	(10.00 / 79.33)	41.43	(21.33 / 64.00)	36.67	(36.67 / 36.67)	3.78	(0.00 / 11.33)	79.83	(34.00 / 100.00)
Percent glides + all pool types	56.00	(20.67 / 90.00)	58.57	(36.00 / 78.67)	63.33	(63.33 / 63.33)	138.33	(102.00 / 156.67)	20.17	(0.00 / 66.00)
Percent all pool types	10.15	(0.00 / 52.00)	2.19	(0.00 / 10.00)	0.00	(0.00 / 0.00)	136.67	(102.00 / 156.67)	1.25	(0.00 / 8.00)
Water flow heterogeneity (fast, smooth, and pool sequence)	0.14	(0.07 / 0.25)	0.14	(0.09 / 0.23)	0.13	(0.13 / 0.13)	0.13	(0.05 / 0.22)	0.02	(0.00 / 0.05)
Fast and slow flow water flow sequence	0.14	(0.05 / 0.25)	0.13	(0.09 / 0.23)	0.13	(0.13 / 0.13)	0.12	(0.04 / 0.19)	0.01	(0.00 / 0.03)
Water surface gradient over reach (%)	0.16	(0.01 / 0.71)	0.08	(0.01 / 0.25)	0.08	(0.08 / 0.08)	0.04	(0.01 / 0.10)	0.05	(0.01 / 0.15)
Channel sinuosity	1.19	(1.07 / 1.33)	1.24	(1.14 / 1.30)	1.20	(1.20 / 1.20)	1.23	(1.11 / 1.35)	1.16	(1.03 / 1.27)