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**Explorando o nicho de peixes de água doce:
Uma abordagem evolutiva e conservacionista em igarapés de terra firme
Amazônicos.**

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Manaus, Amazonas

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Orientador: Jansen Zuanon

Coorientador: Paulo De Marco Jr.

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Sinopse:

Estudaram-se quais as melhores variáveis ambientais para obter informações sobre o nicho Grinneliano de peixes de igarapés Amazônicos. Aspectos da conservação do nicho, conservação e proteção dessas espécies também foram abordados.

Palavras-chaves: Variáveis de macroescala, conservação de nicho, áreas

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Resumo

As principais ameaças aos sistemas e os organismos de água doce são as alterações direta do habitat pelo impacto antrópico. A vulnerabilidade desses ecossistemas tem sido discutida nas últimas décadas, entretanto, pouco se tem feito para a conservação desses sistemas. Hoje em dia o grupo de vertebrados mais ameaçados são os peixes de água doce, a maior riqueza desse grupo está na bacia Amazônica, juntamente com as maiores lacunas de informação, principalmente sobre espécies de peixes de igarapés. A modelagem de distribuição de espécies (MDE) tem se tornado uma importante ferramenta em estudos de ecologia, biogeografia, evolução e conservação, especialmente em áreas com lacunas de informação. Isso é devido ao fato da MDE ser baseada em variáveis climáticas de macroescala que determinam a distribuição dos organismos. Entretanto, pouco se discute sobre o uso dessas variáveis ambientais de macroescala para a modelagem de organismos aquáticos. Sabe-se que os ecossistemas aquáticos são dependentes das paisagens que os cercam, assim, alguns modelos construídos com variáveis de macroescala obtiveram resultados semelhantes aos modelos baseados em variáveis locais para a distribuição de espécies aquáticas. Isso possibilita compreender as exigências ecológicas das espécies podendo auxiliar no entendimento sobre a biodiversidade local e/ou regional, especialmente em áreas pouco conhecidas como os trópicos. Alguns autores argumentam que a diversidade nos trópicos é devida à estabilidade climática dessas regiões, fazendo com que os clados tivessem mais tempo para se diversificar, e atribuem essa diversidade de espécies à conservação de nicho. Essa tendência de espécies filogeneticamente próximas terem o nicho fundamental ou realizado similares é conhecida como Conservação Filogenética do Nicho. Essa característica, de manter o nicho conservado ao longo do tempo, pode determinar em que condições ambientais um táxon de um determinado clado pode ocupar ou tolerar. Por outro lado, espécies que retêm seu nicho similar por longos períodos podem ter dificuldade em se adaptarem a mudanças no nicho, podendo levá-las a extinção, tornando-as mais vulneráveis em relação aos impactos antrópicos. Uma das formas de tentar barrar esse impacto é através das Áreas Protegidas (APs). A região Amazônica possui as maiores APs do Brasil, entretanto, elas não foram idealizadas para proteger organismos aquáticos. Assim, esse estudo teve como um dos objetivos relacionar o nicho Grinneliano dessas espécies com variáveis locais, para obter melhores modelos para essas espécies. Dentro dessa abordagem do Nicho Grinneliano ter uma boa correlação com as características limnológicas, também exploramos a evolução desse nicho ao longo do tempo evolutivo. Por fim, verificamos se as espécies de peixes de

igarapés Amazônicos são protegidas formalmente pelas Áreas Protegidas da Amazônia legal Brasileira, as Megareservas. Uma vez que para a criação e implementação dessas áreas foram somente considerando ecossistemas e organismos terrestres, e áreas de alta pressão antrópica. Assim, as diferentes formas em que o nicho dessas espécies foi explorado mostrou que, apesar de se conhecer pouco sobre esses organismos, eles são altamente vulneráveis aos impactos antrópicos, e precisam ser incluídos nos planejamentos sistemáticos a para conservação da Amazônia.

Abstract

The main threats to freshwater ecosystems and organisms are habitat alteration by anthropic impact. The vulnerability of these ecosystems has been discussed over the last decade; however, little attention has been given to protect these ecosystems. The most threatened vertebrates are the freshwater fishes, whose highest richness is in the Amazon basin, as the widest gap of information, especially for stream species. Species distribution modeling (SDM) has become an important tool in ecology, biogeography, evolution and conservation studies. SDM is based on a set of macroscale variables that determine the distribution of organisms. Thus, a set of environmental variables are used as an input for these models. However, insufficient attention is given to discussing the use of these environmental data for the modeling of aquatic organisms. Freshwater ecosystems are dependent on the surrounding landscape, and some models built with macroscale variables yielded similar results as models based on local variables for distribution of aquatic organisms. The knowledge of species ecological requirements could help understanding the local and/or regional biodiversity. Some authors attribute the high diversity of species in the tropics to conservation niche. They state that the diversity is due to the climatic stability of these regions, and that clades have more time to diversify. This tendency for close related species to have similar fundamental or realized niches is known as Phylogenetic Niche Conservatism. The conservatism of ecological niches could determine environmental conditions in which a taxon of a particular clade can be occupied by dispersing. Conversely, species that retain their niche for long periods of time could have difficulty adapting to environmental changes, and this characteristic could lead them to extinction. Thus, we tested whether the Amazon stream fishes are formally protected by the Amazon Protected Areas (PAs), the Megareserves.

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Introdução Geral

As águas continentais constituem um recurso natural extremamente valioso ecologicamente, culturalmente, economicamente e cientificamente, sendo a conservação e manejo desses sistemas um dos pontos críticos para os interesses de todas as nações e governantes (DUDGEON et al., 2006). As principais ameaças aos sistemas de água doce são a alteração direta por degradação, perda ou fragmentação do habitat; alteração da vazão, mudanças do uso da terra ou alterações na captação de água; exploração por pesca comercial ou esportiva; contaminação; espécies invasoras devido à mudança do ambiente ou introdução de novas espécies; e mudanças climáticas que podem afetar os ciclos hidrológicos (DUDGEON et al., 2006; ABELL; ALLAN; LEHNER, 2007; BARLETTA et al., 2010).

A vulnerabilidade dos ecossistemas de água doce está sendo discutida há algumas décadas (DUDGEON et al., 2006; CASTELLO et al., 2013), entretanto, o planejamento e a gestão dos recursos hídricos é insatisfatório, principalmente no Brasil. Atualmente, os peixes de água doce compõem o maior número de espécies ameaçadas de vertebrados no Brasil, principalmente em relação à perda contínua de habitats (NOGUEIRA et al., 2010). Segundo Nogueira e colaboradores (2010), a Amazônia abriga a segunda bacia hidrográfica no Brasil com maior número de locais críticos em relação à combinação de impactos de barragens, carência de áreas protegidas e perda de habitat.

Apesar de todos os avanços em relação à preservação do bioma Amazônia, com a diminuição dos índices de desmatamento, de emissão de carbono e programa de Redução de Emissões provenientes de Desmatamento e Degradação florestal (REED), pouca atenção tem sido dada ao manejo dos ecossistemas de água doce dessa bacia hidrográfica (CASTELLO et al., 2013). A estrutura em rede dos sistemas fluviais torna esses sistemas altamente vulneráveis, tanto a impactos locais, diretamente nos rios e riachos, quanto a impactos em larga escala no ecossistema terrestre de entorno (CASTELLO et al., 2013). Como as demandas pelos recursos aquáticos aumentaram devido à expansão humana, os sistemas fluviais estão sendo alterados de forma extensiva por represamentos e desvios dos cursos d'água, impactos físicos, químicos e biológicos, para atender às necessidades de água, energia e transporte das populações humanas (NILSSON et al., 2005; CARPENTER; STANLEY; VANDER ZANDEN, 2011).

A bacia Amazônica possui aproximadamente 7 milhões de km² com uma das maiores riquezas de espécies de peixes do planeta (GOULDING; BARTHEM; FERREIRA, 2003; ABELL et al., 2008). Apesar dos ecossistemas aquáticos terem uma extraordinária riqueza de

espécies, alto grau de endemismo e estarem ameaçados por perturbações antropogênicas, esses ambientes ainda são pouco utilizados como alvo em planos de conservação. Isso pode ser devido à lacuna de conhecimento, e de dados sobre a distribuição de organismos de água doce (ABELL et al., 2008). Segundo Malabarba e colaboradores (1998), estima-se que haja aproximadamente 8000 espécies de peixes de água doce neotropicais, e no Brasil há atualmente mais de 2600 espécies válidas (SHAEFER, 1998). A Amazônia abriga a maior bacia hidrográfica do mundo, e, como seria esperado, também possui uma enorme lacuna de conhecimento sobre sua fauna aquática, principalmente sobre a ictiofauna de riachos de floresta, localmente conhecidos como igarapés.

Obter informações sobre a distribuição geográfica das espécies e entender os fatores que influenciam esses padrões pode ajudar muito na mitigação de impactos sobre a biota. Alternativas para essa abordagem são as novas tecnologias representadas por ferramentas de Sistema de Informação Geográfica (SIG), que permitem obter informações de distribuição em macroescala espacial, além da geração e disponibilização de dados ambientais e de ocorrência de espécies, com o acesso às informações disponíveis em coleções biológicas (PETERSON, 2001; ANDERSON; PETERSON; GÓMEZ-LAVERDE, 2002). A modelagem de distribuição de espécies (MDE) tem se tornado uma importante ferramenta em estudos de ecologia, biogeografia, evolução e, mais recentemente, em biologia da conservação e sobre os efeitos ecológicos das mudanças climáticas em curso no planeta (GUISAN; THUILLER, 2005; ARAÚJO; GUISAN, 2006; DINIZ-FILHO et al., 2009; NÓBREGA; DE MARCO JR., 2011). Esses modelos são baseados em dados ambientais de macroescala, que representam os requerimentos ecológicos das espécies, e extrapolam as distribuições das espécies para áreas pouco ou mal amostradas, a partir de pontos de ocorrência confirmada dessas espécies (TÔRRES; VERCILLO, 2012). Assim, a MDE permite analisar potenciais ameaças, direcionar estudos de impactos antrópicos e áreas potenciais para conservação (TÔRRES; VERCILLO, 2012), principalmente em áreas onde há pouca informação disponível sobre as espécies.

A MDE é baseada no nicho Grinnelliano (SOBERÓN, 2007), sendo este definido como o conjunto de variáveis climáticas em escalas de ampla resolução (macroescala) que determinam a distribuição dos organismos, de acordo com intervalos de tolerância que garantam sua sobrevivência e reprodução. Uma das primeiras definições de nicho foi proposta por Grinnel em 1917, como sendo as condições ambientais necessárias para que uma espécie ocorra em um determinado local. Grinnel considerou somente variáveis ambientais abióticas

(variáveis climáticas) e o nicho como o hábitat da espécie. Alguns anos mais tarde, Elton (1927) propôs uma nova definição de nicho como sendo a função ou a posição ecológica de um organismo ou população na comunidade. Essa definição leva em consideração os recursos usados pelas espécies, caracterizando o nicho como função ou nicho trófico.

Em 1957, Hutchinson definiu o nicho como sendo um espaço hipervolumétrico que pode ser dividido em: (1) nicho fundamental, ou seja, as condições ambientais necessárias (fatores abióticos) para que uma espécie mantenha sua taxa de crescimento positiva; e (2) nicho realizado, que leva em consideração as interações bióticas (fatores bióticos) para que uma determinada espécie mantenha sua taxa de crescimento positiva. Essa definição ainda é amplamente utilizada em estudos ecológicos e foi recentemente rediscutida por Holt (2009).

Alguns trabalhos discutem a falta de informações sobre variáveis ambientais locais dos corpos d' água para o estudo de peixes, pois podem representar uma importante limitação na metodologia e, conseqüentemente, afetar os resultados das modelagens. Assim, a obtenção e a inclusão de variáveis locais, como pH, oxigênio dissolvido na água, disponibilidade de nutrientes, profundidade do corpo d' água, combinadas com as variáveis de paisagem, podem melhorar significativamente a qualidade dos modelos (OAKES et al., 2005; DOMÍNGUEZ-DOMÍNGUEZ et al., 2006). Na bacia Amazônica, essas variáveis limnológicas são fortemente afetadas pela geologia e geomorfologia da região. Em 1985 Sioli classificou os tipos de água da Amazônia com base em características limnológicas relacionadas à formação geológica da bacia: *Águas claras*, originárias dos escudos do Planalto Central Brasileiro e escudos das Guianas, possuem pH próximo à neutralidade e condutividade baixa, devido ao fato desses escudos serem muito antigos e sujeitos a muito intemperismo; *Águas brancas*, originárias da porção oeste da Amazônia, sofrem influência dos Andes, possuem pH variando de ligeiramente ácido a levemente básico, e alta condutividade elétrica, devido aos sedimentos que vêm dos Andes; e *Águas pretas*, com pH fortemente ácido e baixa condutividade, devido ao tipo de solo arenoso, percolando a água da chuva juntamente com ácidos húmicos da vegetação ripária. Esses diferentes tipos de água podem ser uma barreira ecológica para algumas espécies de peixes. Além das condições limnológicas, fatores estruturais como largura do riacho e profundidade, e, conseqüentemente, vazão, também influenciam na composição de espécies de peixes (MENDONÇA, et al., 2005). Uma vez que os ecossistemas de água doce são fortemente dependentes das paisagens que os cercam (FAUSH et al., 2002), características da paisagem podem afetar a composição de espécies de peixes. Há vários estudos mostrando que as variáveis de macroescala (escalas regionais, paisagem e/ou mais

ampla) podem afetar a composição de espécies de peixes em assembleias locais (MARSH-MATTHEWS; MATTHEWS, 2000; OBERDORFF et al., 2001; KENNARD et al., 2007; TORRENTE-VILARA et al., 2011). Além disso, modelos construídos com variáveis de macroescala obtiveram resultados semelhantes aos modelos baseados em variáveis locais para a distribuição de espécies aquáticas (KRUSE; HUBERT; RAHEL, 1997; PORTER; ROSENFELD; WATSON; HILLMAN, 1997; PARKINSON, 2000),

Na região da Amazônia Central brasileira, as variáveis de escala regional são sobrepostas às variáveis em escala local, afetando hierarquicamente a composição de espécies de peixes dessa região (MENDONÇA, 2010). Assim, o presente estudo teve como um de seus objetivos verificar a relação entre variáveis locais/limnológicas (pH, condutividade elétrica, temperatura e oxigênio dissolvido na água) de rios e riachos da Amazônia, com variáveis climáticas e geomorfológicas de macroescala, testando seu valor preditivo para uso em modelagens de distribuição de espécies de peixes de igarapés de terra firme.

O entendimento das causas que podem levar à variação geográfica da riqueza das espécies é o que liga os estudos ecológicos e biogeográficos (WILLIG; KAUFMAN; STEVENS, 2003). Há autores que argumentam que para entender a diversidade global, é preciso compreender as exigências ecológicas de espécies próximas evolutivamente (HOF; RAHBEK; ARAÚJO, 2010; HUA; WIENS, 2013), pois acreditam que o nicho influencia na separação dos grupos. Segundo Pulliam (2000), as espécies podem tanto ajustar-se às mudanças no nicho, quanto elas próprias mudarem o seu nicho. Contrariamente, espécies podem manter seu nicho pouco ou praticamente inalterado ao longo de milhões de anos, o que resultaria em conservação do nicho. Alguns autores atribuem a grande diversidade de espécies encontradas nos trópicos à conservação de nicho (CN) (WIENS; DONOGHUE, 2004; HAWKINS; DEVRIES, 2009). Esses autores mostraram que clados de espécies tropicais possuem seus nichos climáticos mais conservados quando comparados a espécies de regiões temperadas, e atribuíram isso à estabilidade dos trópicos, ou seja, menores flutuações climáticas, fazendo com que as espécies tivessem mais tempo para se diversificar (GIEHL; JARENKOW, 2012; HAWKINS; DEVRIES, 2009; WIENS; DONOGHUE, 2004).

Essa tendência de espécies filogeneticamente próximas terem o nicho fundamental ou realizado similares, ou a tendência de espécies mudarem pouco ao longo do tempo, é conhecida como Conservação Filogenética do Nicho (PEARMAN et al., 2008). As relações entre espécies filogeneticamente próximas e ecologicamente similares têm sido investigadas usando duas abordagens: 1) quantificando o sinal filogenético; 2) entendendo a relação entre

semelhanças ecológicas e filogenéticas, ideia que gira em torno da Conservação Filogenética do Nicho ou “*Phylogenetic Niche Conservatism*” (PNC) (LOSOS, 2008).

O sinal filogenético é a tendência de espécies proximamente relacionadas filogeneticamente assemelharem-se mais entre si em relação a uma determinada característica, do que o esperado ao acaso (BLOMBERG; GARLAND, 2002). Assim, sob um modelo evolutivo simples, como o movimento browniano, espécies proximamente relacionadas de uma árvore hierárquica qualquer terão a tendência de serem mais semelhantes (BLOMBERG; GARLAND, 2002). Caso ocorra uma pressão seletiva para a mudança de um caráter, essa “nova” característica que aparecerá na espécie já não estará sob o modelo do movimento browniano (o modelo que seria esperado ao acaso). Com isso, haverá uma perda do sinal filogenético, pois esse caráter estará sofrendo uma pressão evolutiva (BLOMBERG; GARLAND, 2002). Quando esse caráter é o nicho das espécies, esse sinal filogenético passa a representar a conservação filogenética do nicho de uma determinada espécie. Assim, associando informações sobre características do nicho com informações filogenéticas é possível obter um melhor entendimento sobre a dinâmica do nicho de uma espécie (PEARMAN et al., 2008). Alguns mecanismos podem levar à conservação filogenética do nicho. Entre eles, a seleção estabilizadora favorece os indivíduos que vivem no mesmo ambiente e possuem o mesmo nicho que o ancestral, pois a mudança no nicho ancestral diminuiria o “*fitness*” desses organismos. Pleiotropia também tem sido aventada como fator importante, pois o(s) gene(s) que influencia(m) na expansão do nicho também poderiam causar a redução do “*fitness*”; outros fatores aventados são o limite de variação genética de um determinado traço; e fatores bióticos, como predação e competição, os quais não permitiriam que uma espécie colonizasse uma nova área (COOPER, JETZ, FRECKLENTON, 2010).

A conservação de nichos ecológicos pode fornecer informações importantes para a conservação das espécies, pois a partir dessa característica é possível determinar quais condições ambientais podem ser toleradas por táxons de um determinado clado, e, conseqüentemente, quais as regiões que podem ser ocupadas por dispersão, indicando prováveis barreiras ecológicas e/ou geográficas para a sua dispersão (WIENS; GRAHAM, 2005). Além disso, é possível prever cenários ambientais em que as espécies poderão continuar existindo, caso ocorra alguma mudança ambiental (WIENS et al., 2010). Por outro lado, alterações ambientais podem levar ao desaparecimento das espécies em locais específicos ou à sua extinção completa (WIENS; GRAHAM, 2005). A CN também é um

ponto central em estudos de invasões de espécies alóctones, informando sobre locais onde essas espécies podem invadir devido à semelhança das condições ambientais de seus nichos ecológicos originais (LARSON; OLDEN, 2012; PALAORO et al., 2013). Assim, a conservação de nicho pode conferir uma maior vulnerabilidade às espécies de igarapés de terra-firme Amazônicos em relação a impactos antrópicos. Sob essa perspectiva, este estudo testou a hipótese de conservação de nicho em espécies de peixes de pequenos igarapés de terra-firme na Amazônia Brasileira.

A partir das ameaças identificadas aos ecossistemas de água doce (citadas acima) e das características do nicho ecológico das espécies de peixes de igarapés da Amazônia, o presente estudo também abordou o planejamento sistemático para a conservação biológica no Brasil e quais as ações que já foram tomadas para a proteção dessas espécies. A Amazônia legal Brasileira possui aproximadamente 43% da sua área protegidos, em forma de unidades de conservação (UCs) de proteção integral, de uso sustentável e terras indígenas (VERÍSSIMO et al., 2011). Com o intuito de que haja uma sistematização na criação, implementação e manejo das UCs do Brasil, foi criado em 2000 o Sistema Nacional de Unidades de Conservação (SNUC). Alguns anos mais tarde o governo lançou o programa Áreas Protegidas da Amazônia (ARPA), que teve como um dos primeiros desafios reduzir o desmatamento na região (VERÍSSIMO et al., 2011). Dessa forma, grande parte das UCs criadas até 2010 foram implementadas em áreas sob alta pressão antrópica, na tentativa de promover uma diminuição do desmatamento. Apenas algumas poucas UCs foram implementadas em áreas remotas e com foco exclusivo na proteção da biodiversidade (VERÍSSIMO et al., 2011).

Apesar das ameaças, a Amazônia ainda possui grandes áreas remotas de floresta prístina, criando oportunidades para a conservação biológica (PERES, 2005). As UCs da Amazônia são as maiores existentes no Brasil, e grande parte delas possui uma área maior que 1 milhão de hectares, sendo consideradas megareservas. Essas áreas têm o objetivo de cobrir a maior diversidade de ecossistemas possível, manter populações viáveis de grandes predadores e áreas para espécies migradoras, principalmente em regiões onde há grandes lacunas de informação sobre a biodiversidade (PERES, 2005). Entretanto, a imensa maioria das UCs da Amazônia legal Brasileira, além de terem sido implementadas em áreas de pressão antrópica, foram planejadas para a preservação de ecossistemas e organismos terrestres, com a premissa de que, protegendo grandes áreas, também estariam protegendo os ecossistemas e organismos de água doce. Esse não é um problema somente do Brasil, e sim mundial, pois poucos planejamentos sistemáticos de conservação levam em consideração os ecossistemas fluviais

(AMIS et al., 2009; BEGER et al., 2010; LAWRENCE et al., 2011). Assim, fizemos um estudo adicional com o objetivo de verificar se as Megareservas da Amazônia legal brasileira protegem adequadamente a ictiofauna de igarapés. É importante ressaltar que o estado de conservação da maioria das espécies estudadas nesse trabalho nunca foi avaliado segundo os critérios da IUCN (www.iucnredlist.org).

O Projeto Igarapés teve início em 2001, com o objetivo principal de contribuir com o conhecimento ecológico desses sistemas de pequenos corpos d'água (riachos) na Amazônia Brasileira. O projeto desenvolve estudos que visam a avaliar a ocorrência e distribuição das espécies de organismos aquáticos, sua história natural e fatores bióticos e abióticos que possam influenciar a estrutura dessas comunidades aquáticas (www.igarapes.bio.br). Esse projeto possui um banco de dados com aproximadamente 400 pontos de coleta, especialmente bem distribuídos ao longo da Bacia Amazônica, que foram georreferenciados em campo e que empregaram metodologia padronizada para coleta de peixes e tomada de dados sobre parâmetros bióticos e abióticos (MENDONÇA; MAGNUSSON; ZUANON, 2005). Assim, combinando dados obtidos em campo com informações sobre fatores ambientais disponíveis em escala de paisagem para a Amazônia, este estudo utilizou técnicas de modelagem ecológica e uma abordagem macroecológica para estudar os sistemas de igarapés de terra firme amazônicos e sua ictiofauna, a partir de características do nicho Grinneliano, gerando informações sobre o status de conservação dessas espécies.

Objetivos

A presente Tese é dividida em três capítulos principais, cujos objetivos foram:

- Capítulo 01: Testar a relação entre variáveis limnológicas e variáveis macroecológicas para serem utilizadas na modelagem de nicho ecológico de espécies de peixes de igarapés.
- Capítulo 02: Testar a hipótese de conservação de nicho em peixes de igarapés amazônicos, e sua importância para a conservação dessas espécies.
- Capítulo 03: Verificar a efetividade das Megareservas como áreas protegidas para a conservação de peixes de igarapés amazônicos.

Capítulo 1

Evaluating the use of macroscale variables as proxies for local aquatic variables and to model stream fish distribution.

Freshwater Biology (aceito).

Evaluating the use of macroscale variables as proxies for local aquatic variables and to model stream fish distributions

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Abbreviated title: Use of macroscale variables as a proxy for limnological variables

Keywords: aquatic variables, modelling species distribution, stream fish, Amazon, macroscale variables.

Summary

1. The geographical ranges of species are influenced by three components: spatial distribution of environmental conditions, biotic interactions and the dispersal capacity of species. The scarcity of distributional records in vast regions such as the Amazon impedes understanding of fish distribution. Predictive distribution models have emerged as a better alternative to surpass this problem, but the absence of large-scale maps for aquatic variables has been suggested as an important limitation.

2. We aimed to evaluate the use of macroclimatic variables as surrogates for local limnological variables in the Brazilian Amazon. Ordinary least square were used to predict the local habitat variables from climatic and geomorphological information as macroscale variables. Models for six stream-dwelling fish were built in MaxEnt and validated using Area Under Curve and True Skill Statistics (TSS).

3. All local variables were predicted successfully ($R^2 > 0.39$), and MaxEnt models had good suitability using the macroscale variables (TSS higher than 0.70). We conclude that macroscale variables can be effective surrogates for local habitat variables, at least for large-scale analyses on poorly sampled regions such as the Brazilian Amazon.

Introduction

Current understanding of the factors that determine the geographical ranges of species is focused on three main factors which determine the sites that are accessible for colonisation (Soberón, 2007): (1) the spatial distribution of environmental conditions that determine the survival of individuals and the persistence of populations; (2) biotic interactions and the dynamics of resources; and (3) the dispersal capacity of species. This general conceptual model has been used to predict species distributions for a variety of different problems, including the conservation biogeography of individuals or groups of species (Esselman & Allan, 2011; Nóbrega & De Marco Jr., 2011; Rodríguez-Soto *et al.*, 2011), the identification of potential areas of invasion by non-native species (Mata *et al.*, 2010), and the possible response of species to climate change (Araújo *et al.*, 2005; Araújo, Thuiller & Pearson, 2006; Buisson *et al.*, 2010). The methods developed under this approach have captured the attention of many researchers, especially in areas where large gaps in biogeographical information have hindered conservation efforts (Siqueira *et al.*, 2009), such as in the Brazilian Amazon (Buermann *et al.*, 2008).

Species distribution modelling is based on the Grinnellian niche (Soberón, 2007), which is defined as the set of climatic variables at broad resolution scales (hereafter macroscale variables) that determine the distribution of organisms. This view suggests that the dominant filters determining potential areas of occurrence for a given species are macroscale variables, which may include topographical/geomorphological information. Otherwise, the availability of many macroscale variables at higher resolutions (e.g., digital maps with 1 km² to 90 m² pixel resolutions; www.dpi.inpe.br/Ambdata/; www.worldclim.org) has favoured the development of species distribution modelling (SDM) using the ecological niche modelling approach (Peterson & Soberón, 2012). The past 10 years have experienced an increase in studies on predictive modelling for the distribution of

fish and other aquatic organisms. There are studies focusing on priority areas for conservation (Argent *et al.*, 2003; Filipe *et al.*, 2004; Esselman & Allan, 2011), native species conservation (Domínguez-Domínguez *et al.*, 2006), non-native species distribution (Kornis & Zanden 2010) and the testing and comparison of modelling methods (Olden & Jackson, 2002; McNyset, 2005; Oakes *et al.*, 2005), which were considered by Olden *et al.* (2010) as priorities and challenges to the conservation biogeography of freshwater fish. Usually those models are based on macroscale variables, including mean annual temperature, annual precipitation and topographic variables such as altitude (Argent *et al.*, 2003; McNyset, 2005; Oakes *et al.*, 2005; Domínguez-Domínguez *et al.*, 2006). However, several studies have shown that macroscale variables can affect fish species composition in local assemblages (Matthews & Matthews, 2000; Oberdorff *et al.*, 2001; Kennard *et al.*, 2007; Torrente-Vilara *et al.*, 2011). Several studies suggest that models built using macroscale variables perform similarly to models based on local variables for aquatic species distributions (Kruse, Hubert & Rahel, 1997; Watson & Hillman, 1997; Porter, Rosenfeld & Parkinson, 2000). For instance, Kruse *et al.* (1997) found that geomorphologic variables such as slope, altitude and stream width were good predictors of the distribution of trout in Yellowstone Park. Similarly, Watson & Hillman (1997) found landscape and catchment variables to be the most important predictors of the distribution and abundance of bull trout in the western USA. The importance of those macroscale variables in determining species distribution in streams and rivers may arise from the basic arrangement of the landscapes as a continuum of heterogeneous and hierarchical networks shaped by topography, geology and climatic factors (Fausch *et al.*, 2002). Thus, fish distribution and assemblage structure are driven by factors acting at multiple spatial scales (Kennard *et al.*, 2007; Stewart-Koster *et al.*, 2013).

Some studies have discussed the lack of local environmental variables as a significant drawback in species distribution modelling of aquatic organisms. The models for

some species had lower performance, possibly because they are general when compared with macroscale (climatic) variables (Oakes *et al.*, 2005). In such cases, the inclusion of information regarding the water systems at local scales, such as pH and conductivity, could decrease commission errors of the models (Domínguez-Domínguez *et al.*, 2006). For instance, fish from central Amazonia are known to be affected by local variables such as stream dimension, pH, conductivity and dissolved oxygen at local scales (Mendonça, Magnusson & Zuanon, 2005). The use of local variables for species distribution modelling is hindered because large extension maps of local limnological variables, such as pH or conductivity, are rarely available. For instance, the available grid of monitored limnological variables for the Brazilian Amazon has extensive gaps in its spatial distribution (<http://hidroweb.ana.gov.br>), precluding the use of spatial interpolation to provide mapping of these variables.

Nevertheless, some studies have also demonstrated the possibility of inferring local environmental conditions based on similar characteristics at the drainage basin scale (Davies, Norris & Thoms, 2000; Mugodo *et al.*, 2006). Thus, the existence of a strong relationship between local variables and macroscale variables could allow the latter to be used as effective surrogates for the local limnological variables and the ecological processes that those variables may represent. If properly demonstrated, this may also improve the accuracy of SDM models, especially in areas where local environmental variables are unavailable. We therefore tested the assumption that macroscale variables are good proxies for local limnological conditions in one of the more heterogeneous aquatic systems of the world, the Brazilian Amazon basin. We first present support for macroscale variables as surrogates for local variables using a series of regression analyses. We then use those macroscale variables to model the distributions of six fish species and evaluate the accuracy of the resulting models.

Methods

Environmental variables

The Amazon basin is the largest freshwater aquatic system in the world, occupying approximately 7 million km² with around 70% of this area located in Brazil. Pristine rainforests broadly cover one-third to one-half of the floodplains of rivers and streams (Goulding, Barthem & Ferreira, 2003), which are located under the shade of the forest canopy. The water types in the Amazon depend on the geological origins of the rivers and are generally defined as: *clear waters*, found in water courses draining the old Guyana and Central Brazilian shields; *black waters*, originating in forested podzols and coloured by humic acids; and *white waters*, originating in the geologically recent Andean terrains and subjected to increasing intemperism (Sioli, 1985). These main water types have different limnological characteristics and represent the broadest variation of the aquatic environments in the Amazon.

The local variables used in this study refer to limnological factors, including pH, conductivity, dissolved oxygen and water temperature. Data for these variables were obtained from the Brazil National Water Agency (ANA), the “Brasil das Águas” Project (<http://www.brasildasaguas.com.br/>), and the Igarapés Project (J. Zuanon, data not published; www.igarapes.bio.br). The dataset is derived from 600 sampling locations from 1st order streams to very large (14th order) rivers (Fig. 1). The ANA’s database comprises the Hydrological Information System from hydrometeorological monitoring stations. In the Amazon, these data are restricted to 4th order and above rivers (<http://hidroweb.ana.gov.br/>). The sampling of “Brasil das Águas” Project was conducted in 524 Brazilian rivers restricted to rivers above the 3rd order, with more than one standardised sampling for several (but not

all) rivers due to river size variation. The Igarapés Project has approximately 300 standardised sampling sites in the Brazilian Amazon, from 1st to 3rd order streams. Stream order was defined following, Strahler's modification of Horton's scale (Petts, 1994). After combining the sampling points, we used Moran's I to test the spatial autocorrelation of variables (Supplementary, Table 3).

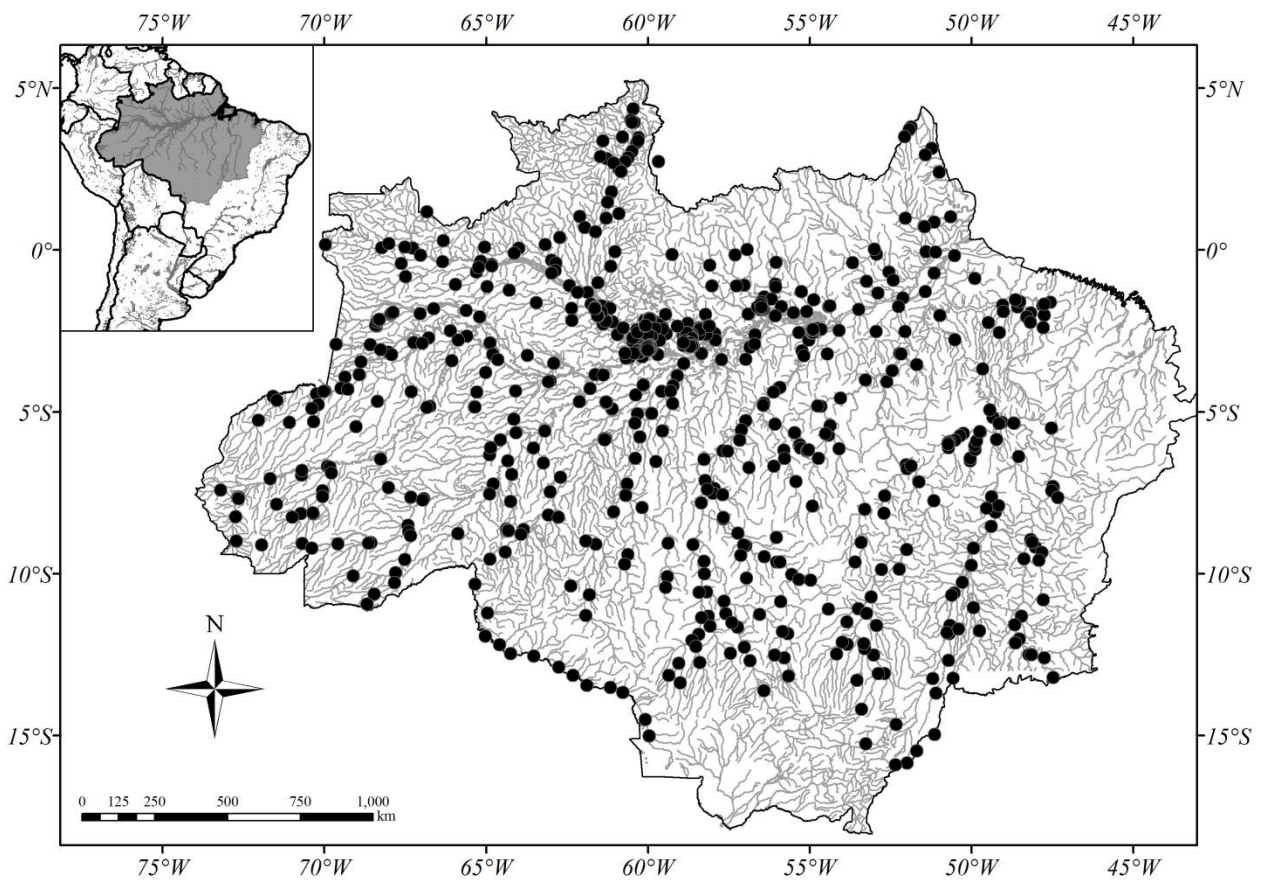


Figure 1: Sample points of local limnological variables in Brazilian Amazon (dark grey area in the inset figure).

Macroscale variables at 1 km² spatial resolution were obtained from AMBDATA (Environmental variables for modelling species distribution), a database from the Brazil National Institute for Space Research (INPE) (www.dpi.inpe.br/Ambdata) which includes all of the Brazilian Amazon surfaces (Table 1). Vegetation characteristics and soil type were

obtained from maps of 1:250.000 and 1:5.000.000, respectively, and then converted to raster format with the same spatial resolution as the other variables. These differences in the scale of the latter variables did not cause any substantial effect on the analytical procedures. The conversion to 1 km² resolution will only produce a distribution of equal values for contiguous cells in the final raster for the variables with coarse resolution.

The variables were chosen by their potential to influence aquatic ecosystems (McNyset, 2009) and their availability in database, and are summarised in Table 1. The annual mean precipitation and annual mean temperature were included to represent the variation in the hydrological periods in the Amazon. The percentage of vegetation cover (sensor MODIS product) and river order were chosen to represent the variation in allochthonous and autochthonous inputs to the aquatic ecosystem.

The terrain slope, soil type and vegetation characteristics are correlated with the amount of nutrients and sediments in streams and rivers and determine the three main water types in the Amazon basin, as described above (Angermeier & Karr, 1983; Sioli, 1985; Goulding *et al.* 2003).

Table 1: Local and macroscale variables used in local variable model analysis.

Macroscale variables	Source
Annual mean temperature (AMT)	AMBDATA/INPE (worldclim), °C, observation from 1950 to 2000
Annual mean precipitation (AMP)	AMBDATA/INPE (worldclim), mm observation from 1950 to 2000
Terrain Slope (SL)	AMDATA/INPE, angular degree.
Vegetation cover percentage (VC)	AMDATA/INPE, MODIS sensor, images from 2000 to 2001

Vegetation type (Veg)	AMBDATA/INPE, SIVAM Project (2002), scale 1:250.000
River Order (Ord)	Derived from MDE, ArcGis, base on hydroshds hydrography, scale 1:250.000.
Soil type (Soil)	AMBDATA/INPE, IBGE, scale 1:5.000.000

Local variables

pH	Igarapés Project, ANA and Brasil das águas Projetc
Electric Conductivity (Cond)	Igarapés Project, ANA and Brasil das águas Projetc
Dissolved Oxygen (OD)	Igarapés Project, ANA and Brasil das águas Projetc
Water temperature (Temp)	Igarapés Project, ANA and Brasil das águas Projetc

Species distribution data

The Igarapés Project has approximately 300 sampling locations distributed throughout the Brazilian Amazon, and approximately 450 fish species were collected and sampled using standardised methodology. The fish were collected with hand nets and small seine nets in a 50-m stream stretch after blocking it with fine-mesh nets (see Mendonça *et al.*, 2005 for details).

Six species were chosen from the Igarapés Project database due to the availability of additional distributional information from the Species Link website (<http://splink.cria.org.br/>). We chose only species that had more than 60 spatially unique points of occurrence. *Copella nattereri* (Steindachner, 1876) and *Pyrrhulina cf. brevis* (Steindachner, 1876) are small Lebiasinidae species very common and abundant in Amazonian streams, and despite the taxonomic uncertainty, we consider it as a taxonomic

entity, based on experience of the author in surveys in different areas of Amazon. The distribution of *C. nattereri* is known to encompass a large portion of the Amazon basin, from the northwestern portion to the lower Amazon, including the Negro River and the upper Orinoco River. *Pyrrhulina* cf. *brevis* (Weitzman & Weitzman, 2003) is found throughout the Amazon basin and occurs with *Erythrinus erythrinus* (Bloch & Schneider, 1801) and *Hoplias malabaricus* (Bloch, 1794) (both Erythrinidae). *Erythrinus erythrinus* is commonly found in small streams, where *H. malabaricus* also occurs, but predominates in lakes and large rivers (Oyakawa, 2003). *Helogenes marmoratus* (Günther, 1863) (Cetopsidae) is a small catfish species usually found in streams distributed throughout the Amazon basin (Vari & Ferraris Jr, 2003) and feeds on allochthonous insects. *Carnegiella strigata* (Günther, 1864) (Gasteropelecidae) is known to occur throughout the Negro River as well as in small-sized tributaries in the upper and middle parts of the Amazon River basin (Weitzman & Palmer, 2003).

Statistical analysis and modelling procedures

We performed the Variance Inflation Factor (VIF) for all of the regression models to evaluate multicollinearity of all of the predictors. This test shows which correlated variable is inflating the model regression, with a VIF higher than 5 indicating collinearity (Zuur *et al.*, 2009). We removed one variable at a time and recalculated the VIF until values were less than 3 (Appendix S1, Table S1). After VIF analysis, we used a Spearman rank-correlation matrix to estimate macroscale variables to evaluate the collinearity among the predictors, allowing non-linear relationships. We excluded variables that present rank-correlations larger than 0.6 (Appendix S1, Table S2). To generate the predictions for limnological variables based on independent macroscale variables, we used the Ordinary Least Squares model (OLS) in the Leaps package in R software (R Development Core Team

2012). We used a model selection approach based on the Bayesian Information Criterion (BIC) and an exhaustive procedure to select the best set of predictor variables. In addition, the accuracy of each best limnological model in predicting local variable values was measured by the regression R^2 values, with predicted values (model value results) vs. observed values (limnological value results). It is important to note that our primary concern is the predictive power of the set of macroscale variables regarding limnological variables and not its explanatory power to select which single variable could explain the variation of water parameters. In fact, we consider macroscale variables to be only proxies of unobserved processes that affect local environmental water parameters.

We used the MaxEnt program for niche modelling. MaxEnt works with presence (occurrence) data only and categorical information. This program estimates the probability of distribution by fitting a function close to the uniform distribution (the probability of maximum entropy) under the restriction of environmental information associated to the occurrence points (Phillips, Anderson & Schapire, 2006). The methods are based on discriminating between the environmental variables of the presence data and the background variation of the environmental variables sampled from 10000 random background (Phillips & Dudík, 2008). One important problem mentioned in recent studies is the low transferability in studies with a high number of occurrence points (Peterson, Papes & Eaton, 2007), explained as a consequence of the higher number of parameters in the resulting models. To circumvent this problem, we controlled the number of parameters in the resulting models by restricting the MaxEnt to linear and quadratic features, similar to Elith *et al.* (2010).

Model evaluation involves predicting niche suitability and comparing the results with a subset of the observed occurrence points that were not included in model training (test subset). We randomly divided the occurrence points into two subsets (subset A and B) for an independent evaluation of the models. We produced a MaxEnt prediction of the distribution

for one subset and used the other to estimate model evaluation measures. Model evaluation was performed with both threshold-independent (e.g., Area Under the Curve - AUC) and threshold-dependent (e.g., True Skill Statistics - TSS) measures, as recently suggested (Liu, White & Newell, 2011). The AUC is obtained by plotting true positives (sensitive values) against false positive values (1-specificity), which is known as the ROC (Receiver Operating Characteristic) curve (Fielding & Bell, 1997). The AUC can then be interpreted as an average sensitivity of all possible values of specificity, producing a global measure of fit for the model. Nevertheless, this method may be subject to problems related to the use of prevalence in the model (Lobo, Jiménez-Valverde & Real, 2008). TSS is less sensitive to prevalence and represents the average rate of prediction success as values varying between -1 and 1 (Liu, White & Newell, 2009). As our approach is entirely based on presence data, TSS and AUC are calculated using background data as pseudo-absence, which is a common procedure in recent SDM literature (see Liu *et al.*, 2009).

Deriving presence and absence from these models requires determination of thresholds that are expected to minimise omission and commission errors. The threshold derived from the ROC is the point that minimises both errors and is considered an equilibrium choice, Minimum Difference Threshold Criterion (MDT) (Jiménez-Valverde & Lobo, 2007). The alternative to ROC is the LPT (Low Presence Training), which minimises only the omission errors and is used mostly for species with a small number of distribution records (Pearson *et al.*, 2006). As observed above, the TSS is dependent on the threshold choice, and we used both measures to test the accuracy of the models.

Results

Environmental variables model

First to third order streams yielded low values for all local variables (water temperature, conductivity, dissolved oxygen and pH) (Fig. 2). These lower order streams are not flood-plains, have a higher slope and altitude, and dense canopy cover. Third order streams showed the highest variance, most likely due to the few available sampling points; 4th order streams are represented by a single sampling point. Streams from the 5th to 8th orders also showed high variance, indicating large variation in limnological characteristics (e.g. differences in water types) among samples. Water temperature was high in streams and rivers of the 5th order and higher, as was conductivity (although with a higher variability) in the 6th order and higher rivers (Fig 2a and 2b, respectively). Dissolved oxygen values were almost uniformly high among the river orders, with a pronounced variance in 3rd order streams (Fig. 2c). The pH showed similar patterns as temperature and conductivity, with a marked increase above the 5th order (Fig. 2d). In general, rivers above the 6th order became limnologically more homogeneous due to the increase in width, discharge and runoff lead to greater buffering of the aquatic system in relation to the variability of local factors influencing the catchment areas of headwater streams (Figure 2).

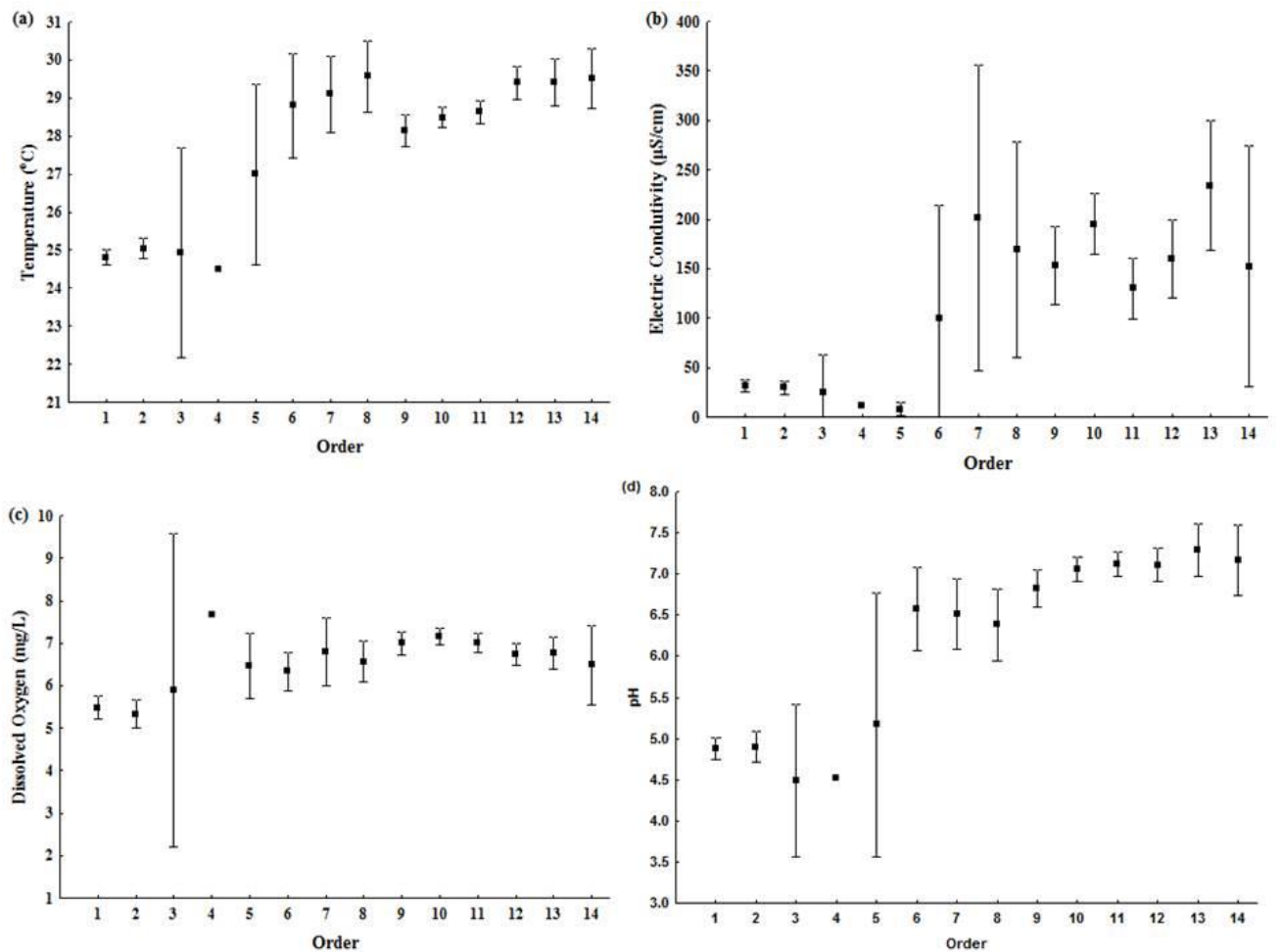


Figure 2: The relationship of river order and mean \pm standard deviation for local limnological variables. (a) Temperature, (b) Electric conductivity, (c) Dissolved oxygen and (d) pH.

Our general statement that macroscale variables could predict local environmental variables is supported by the good general fit of the models (R^2 values ranging 0.53 to 0.79, Table 2). Among the modelled local variables, pH presents the best relationship between the observed and predicted values, with 79% of the variation explained by the model (Table 2, Fig- 3a). For this variable, the best model (BIC = -650) included annual mean precipitation, river order, soil type and vegetation type as component variables (Table 2). The second best relationship was obtained for water temperature ($R^2=0.76$ and BIC = -590, Table 2, Fig. 3b); in this case the variables included in the best model were river order, soil type and vegetation

type. Conductivity was explained by stream order, soil type and vegetation type ($R^2=0.60$ and $BIC = -310$, Table 2, Fig. 3c). The model with the lowest relationship between the observed and predicted values was dissolved oxygen ($BIC = -240$ and $R^2 = 0.53$, Table 2, Fig. 3d). It is important to note that river order, soil and vegetation types were present in all models, and annual mean precipitation in only one model.

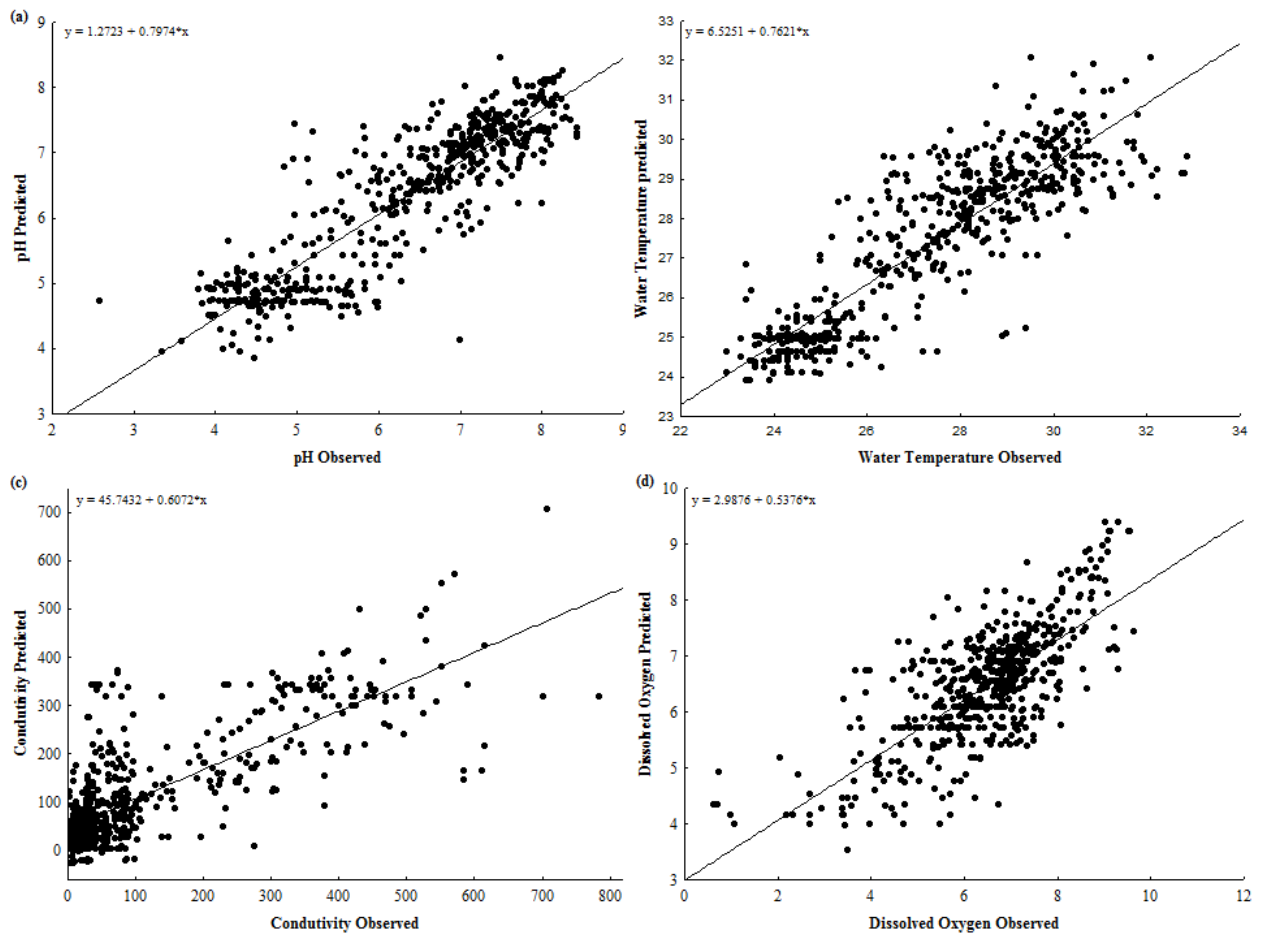


Figure 3: Relationship between observed (local variables) and predicted values for local limnological variables (best model). (a) pH, (b) Water temperature, (c) Electric Conductivity (d) Dissolved oxygen.

Table 2: Best models and macroscale predictors for each local variable. In bold, the Bayesian Information Criterion (BIC) and R^2 for the best models are shown in bold.

	Annual mean precipitation	Annual mean temperature	Vegetation cover	Slope	Soil	Vegetation classification	River order	BIC	R^2
pH	X				X	X	X	-650	0.79
Water Temperature					X	X	X	-590	0.76
Electric Conductivity					X	X	X	-310	0.60
Dissolved Oxygen					X	X	X	-240	0.53

Modelling the distribution of Amazonian stream fish

The AUC values for the model subsets A and B for each species were very similar (Table 3). TSS had more variation between species (0.68 - 0.87). Despite these differences, both indices indicate that the models produced good predictions (Table 3). The species whose occurrence points were concentrated in the Central Amazon (*C. nattereri*, *P.cf. brevis* and *H. marmoratus*) showed high values for AUC and TSS (Table 3, Fig. 4), and *C. nattereri* had very similar models for the subsets A and B with the same species, both for the ROC and LPT thresholds (Fig. 4b). The models also indicated potential areas of occurrence outside central Amazon. *Carnegiella strigata* had occurrence points that were more concentrated in streams of the western Brazilian Amazon but demonstrated results generally similar to the previous species with high AUC and TSS values and similar models for the LTP and ROC thresholds in model A (Fig. 4a). *Erythrinus erythrinus* and *H. malabaricus*, which had broad distributions in the Amazon, had the lowest AUC and TSS values. The models (especially for the LPT threshold) indicate a very large potential distribution area for those species (Fig 4e and 4f, respectively). Considering the six species, the ability of the models to predict distribution points among data subsets was high (0.53 to 1.0).

Table 3: Values of AUC and TSS for models A and B of each species and cross-validation with LPT and ROC. A-B, ROC and LPT for the subset points A and in model B; B-A, the ROC and LPT for the subset points B and in model A. N – Number of occurrences.

Species	N	AUC		TSS		A-B	B-A
		Model	Model	Model	Model	ROC/LPT	ROC/LPT
		A	B	A	B		
<i>Carnegiella strigata</i>	64	0.943	0.944	0.803	0.803	0.53/ 0.78	0.78/0.78
<i>Copella nattereri</i>	88	0.956	0.958	0.843	0.851	1.00/1.00	1.00/1.00
<i>Erythrinus erythrinus</i>	198	0.910	0.924	0.680	0.732	0.71/ 0.95	0.85/0.95
<i>Helogenes marmoratus</i>	155	0.948	0.964	0.824	0.813	0.76/ 0.88	0.91/ 0.91
<i>Hoplias malabaricus</i>	151	0.920	0.899	0.693	0.701	0.53/ 0.83	0.61/ 0.85
<i>Pyrrhulina cf. brevis</i>	140	0.962	0.972	0.838	0.873	0.83/ 0.90	0.89/ 0.97

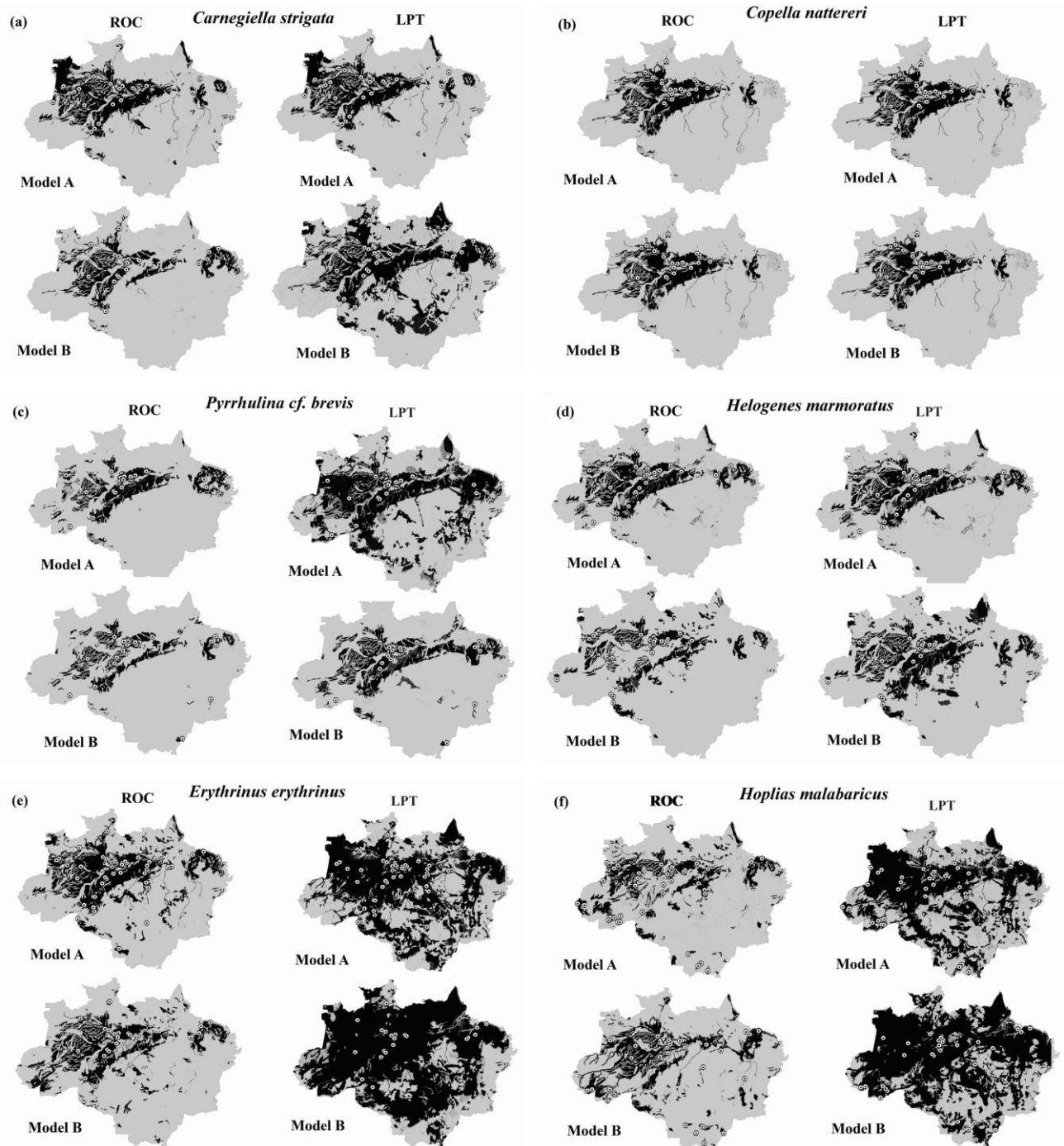


Figure 4: Predictive models for the distribution of fish species using Maxent. Models A and B refer to the partition of training data for modelling (subset points A and B). ROC and LPT were the thresholds used for the most suitable areas. The black areas were niche areas predicted for the model, and the points are the occurrence points used to build the models.

Discussion

Macroscale variables as surrogates for local aquatic conditions

The local variables studied here are all affected by the historical formation of the Amazon basin and are also strongly dependent on its surrounding forest. The soil in the Amazon is overall of low fertility, yet its vegetation cover is the main source of energy and nutrients for the aquatic environment (Sioli, 1985; Goulding *et al.*, 2003). The organic matter inputs to rivers and streams originate from upper and lateral stream catchments and depend on the riparian vegetation and the connection to floodplain areas. The characteristics of the riparian vegetation can differ along the river and catchment area, which could also affect water quality (Kawaguchi, Taniguchi & Nakano, 2003; Dudgeon, 2008). Many observed differences between the limnological conditions of different rivers are associated with catchment geomorphology. The soil type could be a surrogate for geomorphological conditions and an important variable to distinguish between subregions in the Amazon, as was evident from our results. Factors such as soil type, geological formation and vegetation type could change the structure, function and quality of these water bodies, which explains the observed relationship with local variables at broad scales. Limnological condition in the Amazon basin are strongly related to its geological formation, resulting in the different water types. Finally, river size (represented by its hierarchical order) is another variable that reflects the structure of the aquatic ecosystem; as order increases, the system changes from almost exclusively allochthonous sources of energy and nutrients to autochthonous sources of energy, with an increase in the importance of aquatic primary productivity to the structure of its food chains (Vannote *et al.*, 1980). First order forest rivers are allochthonous systems, closely dependent on the surrounding vegetation as a source of energy and nutrients (Kawaguchi *et al.*, 2003). Otherwise, as river width increased with increasing order, the

importance of direct sunlight to the ecosystem also increases, and the system becomes autochthonous (Vannote *et al.*, 1980). However, local aquatic conditions are also affected by many other factors acting at small spatial scales, such as soil deposition, canopy cover, and stream width and depth, especially in small streams. Therefore, our results suggest that macroscale variables could capture the effect of local aquatic variables and thus allow the application of the current general understanding of the Grinnellian niche (Soberón, 2007) to estimate distribution maps for Amazonian stream fishes. It is important to highlight that most variables selected by the OLS models are categorical. This could cause limitations in the choice of the SDM technique because only MaxEnt (Phillips & Dudík, 2008) and GLM based-techniques (Elith & Graham, 2009; Syphard & Franklin, 2009) were specially designed to handle categorical variables.

In a study conducted in the upper Murrumbidgee River in Australia, local stream characteristics were successfully predicted using macroscale information on the geology, alkalinity and catchment area (Davies *et al.*, 2000). A similar study performed on three hydrographic basins in southwest Queensland, Australia (Mugodo *et al.*, 2006), using river order, longitude, source distance and altitude, predicted five local habitat variables with R^2 values greater than 0.2 between the observed and predicted variables. Our results showed that macroscale variables could provide even higher predictive power for limnological parameters (R^2 always higher than 0.53) in the Amazon. Previous studies have discussed the importance of geomorphologic and landscape variables that reflect the catchment structure in species distribution of fish (Kruse *et al.*, 1997; Watson & Hillman, 1997). Comparing the SDM of fish species using solely large-scale variables vs. large scale variables and local variables, Porter *et al.* (2000) showed that large scale variables adequately predict fish species distributions in the Blackwater Drainage in Canada.

Species distribution studies of fish or aquatic organisms are usually conducted at geographical scales significantly smaller than the Amazonian approach employed here (Oakes *et al.*, 2005; Domínguez-Domínguez *et al.*, 2006; Buisson, Blanc & Grenouillet, 2008; Esselman & Allan, 2011; Grenouillet *et al.*, 2011). Due to its vast size and remoteness, the Amazon basin has large gaps in information describing species distributions, biological data and hydrological data. According to Abell *et al.* (2008), the Amazon basin is one of the richest basins of the world, with more than 200 endemic freshwater fish, the majority of which have low or fragmented biogeographical information. Thus, the use of broad-scale environmental variables may allow us to generate species distribution models for those species to prioritise inventory studies and to determine new conservation areas to protect riverine fish species. The SDM can also provide information on habitat requirements, hotspot biodiversity, inventory, and the management of vulnerable areas of habitat change on a large scale (Porter *et al.*, 2000). Once we large gaps in information for the Amazon basin, we will be able to predict fish species distributions and thus to contribute to the conservation of fish species and the Amazon ecosystem.

Modelling stream fish species across the Amazon basin

Terrestrial macroclimatic and topographic variables have been used for modelling fish species distribution (Argent *et al.* 2003; Domínguez-Domínguez *et al.* 2006; McNyset, 2005; Oakes *et al.* 2005). However, few of these studies discuss how these variables could reflect local aquatic conditions. Since our macroscale variables appropriately reflect the local limnological conditions, their use reflects factors related to local conditions and allows us to better generate fish species distributions models. This could be due to most of these species are insectivorous and have strong dependence of the riparian vegetation surround.

The hatchet fish *Carnegiella strigata*, the pencil fish *Copella nattereri* and *P. cf. brevis*, and the leaf catfish *Helogenes marmoratus* demonstrated the best models. These species occur almost exclusively in pristine forest streams and are considered habitat specialists. The model subsets A and B were compared for each species, and both the ROC and LPT were similar in terms of range and area. Their original occurrence points are concentrated in the central-western Amazon, but all subset models show other suitable areas for these species in the eastern Amazon (Figure 4). The areas that lack records of occurrence for the analysed species may represent simple sampling gaps but could also harbour sister species (e.g., Raxworthy *et al.*, 2003). For instance, *Copella nattereri* seems to be replaced by *Copella arnoldi* in the Brazilian Amazon east of the Tapajós River (JZ, pers. obs.), and the absence of data regarding species of *Pyrrhulina* and *Carnegiella* in well sampled small streams of eastern Amazon suggests that similar replacements (eg. Raxworthy *et al.*, 2003) (or maybe undisclosed sister species) may be expected.

The Erythrinidae harbours species that occur in many different habitats, such as lakes, lagoons, and small and large rivers (Oyakawa, 2003). *Hoplias malabaricus* has the widest distribution of this family, occurring in streams and large rivers throughout the Amazon basin (as well as in most tropical and subtropical South American basins). The projected maps of *Hoplias malabaricus* and *Erythrinus erythrinus* showed wide distributions in the Amazon basin (Figure 4), but their models had low performances. These results could be expected as these species have a broad tolerance to changing environmental conditions and have low habitat specificity. In this case, models do not have enough accuracy to capture the requirements of species, and these intrinsic aspects of widespread species may generate models with lower TSS and AUC values, as observed in other studies (Stockwell & Peterson, 2002; Lobo *et al.* 2008).

In conclusion, although two species were not represented by strongly fitted models, in general we can use macroscale variables to build species distribution models and generate information about the biogeographic distribution for Amazon stream fishes.

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Supporting Information

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

Appendix S1. Collinearity and spatial autocorrelation among variables

The collinearity among quantitative variables was tested using the variance inflation factor (VIF) in Spatial Analysis in Macroecology (SAM) software (Table 1). According to (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), values between 3 to 5 are acceptable. For this analysis, we removed one variable at a time until the values were less than 3. Although the VIF values were accepted, we chose to do the Spearman analysis (table2). Variables that yielded values >0.6 and deemed the ecological context were removed as a predictor to model analysis.

Spatial autocorrelation analysis was done with the residuals for each of OLS best models. To do so, we performed the Moran's I. This analysis was done using SAM, and the first class was the only one yielding autocorrelation >0.2 . This is expected due to the geomorphological formation of the Amazon

Table 1: The variance inflation index (VIF) for macroscale variables and the standard coefficient of linear regression.

	pH		Conductivity				Dissolved Oxygen				Temperature					
	VFI	Coef	VFI	Coef	VFI	Coef	VFI	Coef	VFI	Coef	VFI	Coef	VFI	Coef		
Vegetation cover	1.302	-0.308	1.238	-0.352	1.302	-0.183	1.238	-0.116	1.302	-0.28	1.238	-0.281	1.302	-0.33	1.238	-0.36
Annual mean temperature	2.308	-0.284	1.051	-0.292	2.308	-0.465	1.051	-0.100	2.308	-0.044	1.051	-0.069	2.308	-0.387	1.051	-0.091
Slope	1.173	-0.007	1.128	0.017	1.173	-0.108	1.128	-0.190	1.173	-0.037	1.128	-0.033	1.173	0.007	1.128	-0.014
Annual mean precipitation	4.364	0.072	1.311	-0.191	4.364	-0.545	1.311	0.073	4.364	-0.032	1.311	-0.053	4.364	-0.001	1.311	0.005
Altitude	2.646	-0.089			2.646	-0.378			2.646	0.034			2.646	-0.499		
Walsh index	4.776	-0.376			4.776	0.617			4.776	-0.011			4.776	-0.219		

Table 2: Spearman analysis of collinearity among quantitative macroscale variables.

Macroscale Variables	Vegetation cover	Altitude	Slope	Annual mean precipitation	Annual mean temperature	Walsh index
Vegetation cover		-0.13650	-0.13361	0.39741	0.06215	0.46052
Altitude	-0.13650		0.24512	-0.40738	-0.62099*	-0.47677
Slope	-0.13361	0.24512		-0.31737	-0.12592	-0.44579
Annual mean precipitation	0.39741	-0.40738	-0.31737		0.06500	0.83535*
Annual mean temperature	0.06215	-0.62099*	-0.12592	0.06500		0.22921
Walsh index	0.46052	-0.47677	-0.44579	0.83535*	0.22921	

*Values >0.6

Table 3: Moran's I from residuals values from best model for each local variable, significant spatial autocorrelation $p < 0.005$.

Class	pH		Water temperature		Conductivity		Dissolved Oxygen	
	Moran's I	P	Moran's I	p	Moran's I	p	Moran's I	p
1	0.231	0	0.14	0	0.102	0	0.16	0
2	0.106	0	-0.003	0.924	0.021	0.024	0.044	<.001
3	0.059	<.001	0.004	0.572	0.065	<.001	0.094	0
4	-0.022	0.041	0.023	0.014	-0.012	0.333	0.07	0
5	-0.033	0.002	-0.049	<.001	-0.012	0.318	0.005	0.523
6	-0.046	<.001	0.009	0.271	0.013	0.142	-0.002	0.995
7	-0.065	<.001	-0.032	0.003	-0.006	0.67	-0.034	0.002
8	-0.02	0.076	-0.037	<.001	0.004	0.574	-0.013	0.258
9	-0.025	0.022	0.009	0.287	<.001	0.896	0.034	<.001

10	-0.021	0.057	0.016	0.083	0.003	0.64	-0.017	0.147
11	0.012	0.184	-0.021	0.059	0.022	0.023	-0.017	0.127
12	-0.01	0.403	-0.01	0.438	-0.01	0.416	-0.035	0.001
13	-0.022	0.051	-0.023	0.035	0.038	<.001	-0.022	0.045
14	0.007	0.379	-0.015	0.199	-0.002	0.985	-0.016	0.173
15	-0.037	<.001	-0.002	0.939	-0.031	0.004	-0.032	0.003
16	-0.047	<.001	-0.016	0.163	-0.05	<.001	-0.08	0
17	-0.057	<.001	-0.001	0.966	-0.043	<.001	-0.094	0
18	-0.044	<.001	-0.004	0.817	-0.076	0	-0.071	<.001
19	-0.006	0.654	-0.027	0.012	-0.038	<.001	-0.038	<.001
20	-0.006	0.378	0.003	0.588	-0.021	0.038	0.03	<.001

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Capítulo 2

Phylogenetic niche conservatism in freshwater Amazon stream fishes.

Manuscrito em preparação para *Global Ecology and Biogeography*.

Phylogenetic niche conservatism in freshwater Amazon stream fishes

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Abstract

Aim

Amazon non-flooded streams constitute a dense hierarchical river network under the forest canopy with a poorly known, rich fish fauna. Here we investigate the niche conservatism hypothesis in Amazon stream-dwelling species

Location

Brazilian Amazon basin

Methods

We carry out analyses on three major fish orders from the Neotropical region. The information about Grinnelian niche was extracted from macroscale variables using species occurrence points. We used the outlying mean index for niche traits and performed phylogenetic analysis with Moran's I, Phylogenetic Eigenvector Regression and Phylogenetic Signal Representation.

Results

There is low phylogenetic structure among orders and no significant phylogenetic pattern within individual orders. The PSR analysis also shows a low niche evolution both among and within orders.

Main conclusions

Despite of Amazon basin formation, the differentiation of stream fishes is addressed by local habitat requirements. Niche conservatism and stability could increase the risk of species extinction in face of the impact of deforestation, dams and climate change. Once such

impacts are increasing in the Amazon, the fishes from non-flooded stream could be highly threatened.

Keyword: Grinnellian niche, OMI, phylogenetic signal, fish richness, fish evolution, Amazon evolution, conservation.

Introduction

Freshwater ecosystems are affected by the global crisis in biodiversity (Abell, 2002), and have become one of the most threatened ecosystems in the world in face human impact (Dudgeon *et al.*, 2006). Obviously, this directly affects the conservation of all freshwater biodiversity. Freshwater organisms are constrained by the surrounding landscape which limits their dispersal both within and among drainages, and which also isolates populations (Olden *et al.*, 2010). Freshwater ecosystems are nested hierarchical networks and, as such, could constrain the ability of species to respond to environmental change (Faush *et al.*, 2002). The distribution patterns of freshwater fishes are strongly related to the origin and geological formation of rivers (Lundberg *et al.*, 2010), and the combination of environmental characteristics and complex paleogeographical processes make these ecosystems rich in endemic species (Abell *et al.*, 2008). At the same time, species of freshwater fish are vulnerable to human impacts (Faush *et al.*, 2002; Dudgeon *et al.*, 2006), and species with a small body-size seem to be specially affected (Olden *et al.*, 2007).

The Neotropical region contains approximately 25% of the world's freshwater fish diversity, with the Amazon basin harboring the majority of the species richness, estimated to be near 2.000 species (Winemiller *et al.*, 2008). Nevertheless, explaining why tropical regions hold the greatest number of species in many taxa continues to be unresolved. Some

researchers attribute the high species richness found in the Amazon to its complex historical formation (Silva & Patton, 1998; Albert *et al.*, 2005; Albert *et al.*, 2011a; Ribas *et al.*, 2011). The history of the Amazon basin formation is still remains debated, especially about the timing of its modern configuration (Hoorn & Wesseling, 2010; Latrubesse *et al.*, 2010). Some studies state the higher freshwater diversity in Neotropical region, especially in the Amazon basin, could be due to its old age and environmental stability (Albert *et al.*, 2005; Albert *et al.*, 2011a). Understanding the causes driving the geographic variation in species richness is one of the main questions linking ecology and biogeography (Willig *et al.*, 2003). Some authors state that to understand the global diversity it is important to know whether closely related species share ecological requirements (Hof *et al.*, 2010; Hua & Wiens, 2013). The tendency of closely related species having similar ecological or environmental requirements is known as Phylogenetic Niche Conservatism (PNC) (Peterson, 1999; Blomberg & Garland, 2002; Wiens & Graham, 2005; Pearman *et al.*, 2008), because many aspects of the species' fundamental niche are retained over time (Wiens & Graham, 2005).

Niche conservatism may affect species conservation because it could also play a role in limiting the species' capacity to adapt to different climatic conditions (Peterson, 1999; Wiens & Graham, 2005; Olden *et al.*, 2010). For example, if the niche of old clades has been conserved over a long time, and the rates of adaptation to conditions beyond the niche's range is slow, environmental change could lead to the extirpation of species in particular locations or, ultimately, to their extinction (Wiens & Graham, 2005). Niche Conservatism is also a central point in studies of species invasions by informing about potential locations where a non-native species could become invasive and could establish itself owing to the similarity of the local environmental conditions to their original niches (Olden *et al.*, 2010, Larson & Olden, 2012; Palaoro *et al.*, 2013).

The orders Characiformes, Siluriformes and Gymnotiformes are monophyletic and represent almost 80% of freshwater fishes in the Neotropical region. These are very old and widespread groups originated in the Paleocene, which inhabit all freshwater ecosystems (Albert *et al.*, 2011b). Amazon upland first- and second-order streams, locally known as *igarapés de terra-firme*, run under pristine forests, and represent a dense hierarchical river-network under the canopy, home to a fish fauna still poorly known. Most fish found in these streams have a small body-size and low vagility. Their distributions are normally constrained by drainage basins (Albert *et al.*, 2011b). Here, we aim to test whether there is niche conservatism in Amazon stream fish species among and within the three major orders of freshwater fish occurring in the Neotropical region.

Methods

Species and environmental data

We searched the literature for phylogenetic information of the three most abundant orders of freshwater fishes in the Neotropical region: Characiformes, Siluriformes and Gymnotiformes (search on Web of Science, <http://wokinfo.com/>), and Google Scholar, <http://scholar.google.com.br>, using the keywords phylogeny and/or the names of the orders and/or families and/or species of each taxon in the Igarapés Project database (e.g. “phylogeny and Characiformes” and/or “phylogeny and Erythrinidae” and/or “phylogeny and *Erythrinus erythrinus*”). A total of 14 studies were used in this study (listed in the supplementary material) that proposed topological relationships for some of the species within our three selected orders. The information obtained from such studies did not provide data on the timing of events or groups’ origins. Thus, we manually assembled the proposed relationships

into a purely topological, composite phylogeny by setting branch lengths equal to one in Mesquite 2.75 software (Maddison & Maddison, 2011). (Figure 1 S1).

To assemble the composite phylogeny, we considered only those species known to have distribution within the Amazon stream network. For this, we focused on species with more than five occurrence points within the Igarapés Project database (see <http://www.igarapes.bio.br>), resulting in a final set of 73 stream dwelling species. This included 21 species of Characiformes, 37 Siluriformes and 15 Gymnotiformes (Table 2 S1). The Igarapés Project has approximately 400 sampling locations distributed throughout the Brazilian Amazon, sampled with standardized methodology (see Mendonça *et al.*, 2005 for details). In addition, we gathered occurrence information from the Species Link website (<http://splink.cria.org.br/>) to improve the distributional data of our final species set, resulting in a total of 2060 occurrence points for all species from both databases.

Environmental (large scale) variables correlated to local aquatic variables were based on Frederico *et al* (in press; See Chapter 1 of this Dissertation), allowing us to describe the Grinnelian niche (Soberón, 2007) for the selected Amazonian stream fishes. This approach is based on the intrinsic collinearity of many limnological variables and macro-climatic and macro-topographical variables (and also the collinearity among those macro-variables) to choose a best set of environmental layers to model stream-dwelling species. To represent the variation in the hydrological periods of Amazonian streams and rivers we used the climatic variables annual mean precipitation (AMP), annual mean temperature (AMT), seasonality of precipitation (SP), and seasonality of temperature (ST), obtained from WorldClim (global climate data database, www.worldclim.org). We used terrain slope and soil type as geomorphological variables correlated with the amount of nutrients and sediments in streams and rivers (Angermeier & Karr, 1983; Sioli, 1985; Goulding *et al.*,

2003), respectively obtained from Hydro 1k, an spatial database about hydrological information (<http://eros.usgs.gov/>), and Food and Agricultural Organization of the United Nations - FAO. The hydrological variable chosen to represent stream flow and orders (Strahler, 1952) was flow accumulation (Hydro 1k). All these macroscale variables were analysed in a grid with 4X4km resolution.

Niche analysis

To describe the species' niches in an operational form using the macroscale variables above, we used the Outlying Mean Index (OMI; Dolédec *et al.*, 2000). This index allowed us to obtain measures of niche position and breadth occupied by each species within the multivariate niche space described by all species (Doledec *et al.*, 2000). OMI is a multivariate ordination analysis that measures the distance between the mean environmental conditions used by the species (marginality), and the average environmental conditions of the total sampled area (environmental "hyperspace") (Dolédec *et al.*, 2000). This analysis provides information about niche marginality (average distance to hyperspace center, axis score (niche position in hyperspace), tolerance (niche breadth), niche inertia (an estimate of niche overlap) and residual variation (the variation in the niche breadth unrelated to the variables included in the model) (Dolédec *et al.*, 2000; Gouveia *et al.*, 2014). We used the tolerance value and the score of the first axis resulting from the OMI analysis as estimates the species' niche breadth and niche position, respectively.

Niche Conservatism Analysis

Niche conservatism was evaluated for species within each order using two statistical approaches. Owing to the lack of temporal resolution (i.e. branching times) in our assembled phylogeny, we followed a statistical approach for testing the strength of phylogenetic

conservatism in the species' niche properties (breadth and position). First, we calculated a global index of phylogenetic autocorrelation as a measure of trait structure (i.e. species' niche breadth) throughout the phylogeny based on the Moran's autocorrelation index I (Gittleman & Kot, 1990). This procedure quantifies the association between trait values observed on the species as a function of their (phylogenetic) distance (Gittleman & Kot, 1990). This generates mean expected values of I and its variance in the absence of phylogenetic autocorrelation, thus allowing testing the null hypothesis of the absence of phylogenetic similarity among species (Paradis, 2012). The Moran's I index varies from +1.0, when closely related species are more similar in their trait values, to -1.0, when distantly related species are more similar. We assumed phylogenetic niche conservatism involving inheritance from a common ancestor if niche characteristics of species were positively autocorrelated across the phylogeny (Diniz-Filho *et al.*, 2012a)

In addition, we also applied a phylogenetic eigenvector regression (PVR; Diniz-Filho *et al.*, 1998) to estimate the amount of phylogenetic signal in the variation of species' niche properties. Under PVR analysis, the magnitude of phylogenetic signal can be estimated with the coefficient of determination (R^2) derived from a multiple regression model in which phylogenetic eigenvectors are used as predictor variables to explain the variation in species' trait values (Diniz-Filho *et al.*, 2012a). Such phylogenetic eigenvectors are obtained from a Principal Coordinates Analysis (PCoA) of the phylogenetic distance matrix (Diniz-Filho *et al.*, 1998). The eigenvectors resulting from the PCoA are then selected for modeling purposes. Here we followed Diniz-Filho and collaborators (2012b) and selected those phylogenetic eigenvectors for each phylogeny that controlled for autocorrelation in the model's residuals (i.e. the set of eigenvectors for which the model's residuals no longer showed significant autocorrelation at the 0.05 level using Moran's I index). In short, the

phylogenetic eigenvectors represent the pattern of species' relationships at distinct hierarchical levels throughout the phylogeny and the R^2 of the multiple regression model expresses the amount of variation in the species' trait explained by phylogenetic structure (Diniz-Filho *et al.*, 2012a). PVR analysis does not assume an explicit evolutionary model, thus allows the absence of branch length information when modeling phylogenetic structure (Diniz-Filho *et al.*, 1998; Diniz-Filho *et al.*, 2012a,b). Moreover, PVR has been shown to perform as well as other comparative methods (Machac *et al.*, 2011; Diniz-Filho *et al.*, 2012a) and better than autocorrelation methods when applied to small sample sizes (Diniz-Filho *et al.* 1998). Thus, the PVR approach was particularly suited to evaluate our questions given our data, rather than trying to apply more complex approaches requiring more detailed phylogenetic information (Diniz-Filho *et al.*, 2012a).

Finally, we applied an extension of the PVR approach to graphically represent trait variation across a phylogeny. The Phylogenetic Signal Representation (PSR) curve (Diniz-Filho *et al.*, 2012c) can be used to analyze a trait's intrinsic evolutionary rate over a phylogeny and identify more complex patterns of phylogenetic signal including non-stationarity (i.e. different patterns of particular subclades within a phylogeny; Diniz-Filho *et al.* 2010). PSR curves are constructed using the eigenvectors from sequential PVR models (as explained above) in which the model fit (R^2) of successive PVRs of accumulated eigenvectors are plotted against the accumulated percentage of their corresponding eigenvalues (λ) describing their phylogenetic representation (Diniz-Filho *et al.*, 2012b; Bini *et al.*, 2014; Gouveia *et al.*, 2014). The shape of the PSR curve can be informative about the trait's model of evolution (Brownian motion vs. Ornstein-Uhlenbeck [OU] process) across the phylogeny. A 45° reference line indicates evolution under Brownian motion whereas curves below this line may be indicative of stronger phylogenetic signal, with divergence

slower than Brownian motion and responding to an OU process, and curves above the reference line indicates faster divergence (i.e. trait evolution) (see Diniz-Filho *et al.*, 2012b for details on PSR calculation and interpretation). Moreover, shifts along the PSR curve's shape can be indicative of non-stationarity in which different subclades present different phylogenetic structures. All niche and phylogenetic analyses were done in R 3.0.1 (R Development Core Team 2013) using the customized made functions and R packages: ape (Paradis, 2012), ade4 (Chessel *et al.*, 2004), picante (Kembel *et al.* 2009), and PVR (Santos *et al.* 2012).

Results

We gathered data for the selected 21 species of Characiformes, 37 of Siluriformes and 15 of Gymnotiformes present in Amazonian streams. These species are well distributed throughout the phylogeny (Figure 1 S1). Low OMI values were observed for almost all species, resulting that all species have Grinnellian niches near the centroid of their corresponding environmental space, suggesting small differences among them (Figure 1). The tolerance or niche breadth values within Characiformes have varied from 0.35 to 17.39, with the highest values in *Myloplus rubripinnis* (Table 2 S1). Despite their high values for niche breadth, this species did not show high values of niche position. Among the Characiformes the higher OMI value was observed for *Leporinus klausewitzii*, an omnivorous species of Anostomidae.

The tolerance or niche breadth values within Siluriformes (varying from 0.18 to 13.64) were similar among the analyzed species (Table 2 S1). Two minute species of catfish showed the highest value for niche breadth and OMI, respectively *Scoloplax* and *Stauroglanis gouldingi*, a small catfish (2,7cm) from the Trichomycteridae family.

Species of Gymnotiformes showed the lowest niche breadth values, ranging from 0.20 to 3.86. Almost all species within the Gymnotiformes had low niche breadth values, implying small Grinnellian niche breadths, with the higher OMI value for *Gymnotus pendanopterus*, a widely distributed species of the Gymnotidae.

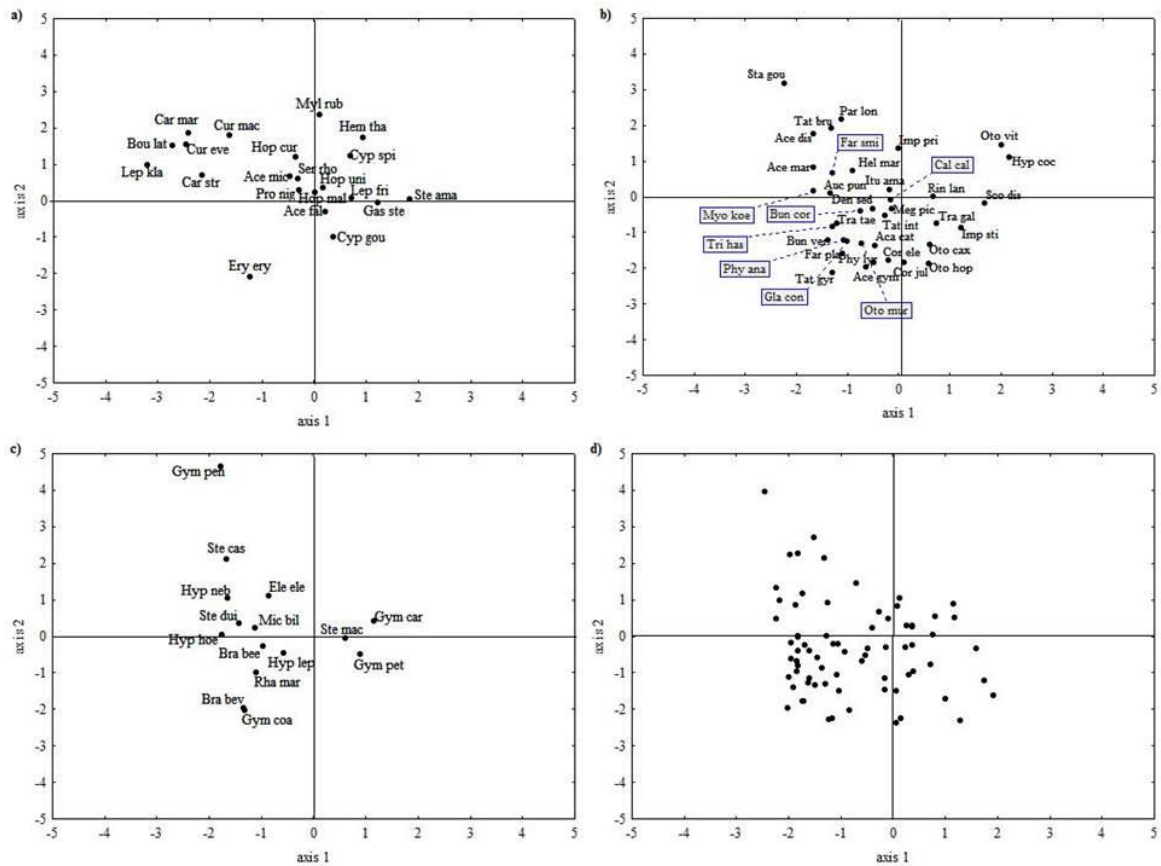


Figure 1: Position of species niche (OMI). a) Characiformes; b) Siluriformes; c) Gymnotiformes; d) all orders together.

Global Moran's I index values within orders were low and not significantly different from the expected by chance (Table 1). Characiformes had negative values of Moran's I for both niche breadth and niche position (-0.041/-0.041). Siluriformes had a negative index for niche breadth (-0.039) and a positive one for niche position (0.031), whereas Gymnotiformes

showed a positive index for niche breadth (0.007) and a negative one for niche position (-0.079). Taken together, Moran's *I* values are low and imply that niche similarity among closely related species does not tend to decrease with phylogenetic distance when species are compared within orders. When comparing species among the three orders, Moran's *I* values were positive and significant for both niche breadth and niche position (0.020/0.039) (Table 1), thus implying phylogenetic structure despite the low Moran's *I* values.

Results of the PVR analyses within orders did not show significant phylogenetic signals for neither breadth or position (Table 1). These results indicate that there is no phylogenetic structure of niche breadth and position within the individual orders. Among orders there was a low significant phylogenetic signal for both niche breadth and niche position ($R^2=0.146$, $p=0.011$ and $R^2=0.16$, $p=0.001$, respectively) (Table 1). The PSR analyses within and among orders suggested slow niche evolution for both traits, niche breadth and niche position, with curves arranging below the 45°-reference line (Figures 2 and 3). Therefore, the phylogenetic results (Moran's *I*, PVR and PSR) are in agreement with a model of slow niche evolution and potential niche conservatism.

Table 1: Global Moran's *I* coefficient and PVR coefficient of determination R^2 and p-values. Breadth – Moran's *I* for niche breadth. Position – Moran's *I* niche position. DF-degrees of freedom. Values marked * and in bold indicate significant p-values (≤ 0.05).

Orders	Global Morans's <i>I</i>					PVR				
	breadth	p	position	P	R2	DF	p	R2	DF	p
					breadth			position		
Characiformes	-0.041	0.769	-.041	0.877	0.244	17	0.179	0.069	17	0.739
Siluriformes	-0.039	0.019*	0.031	0.055*	0.008	33	0.963	0.052	33	0.616
Gymnotiformes	0.007	0.138	-0.079	0.879	0.412	11	0.107	0.220	11	0.397
All orders	0.020*	0.005	0.039*	0.000	0.146*	69	0.010*	0.161	69	0.006*

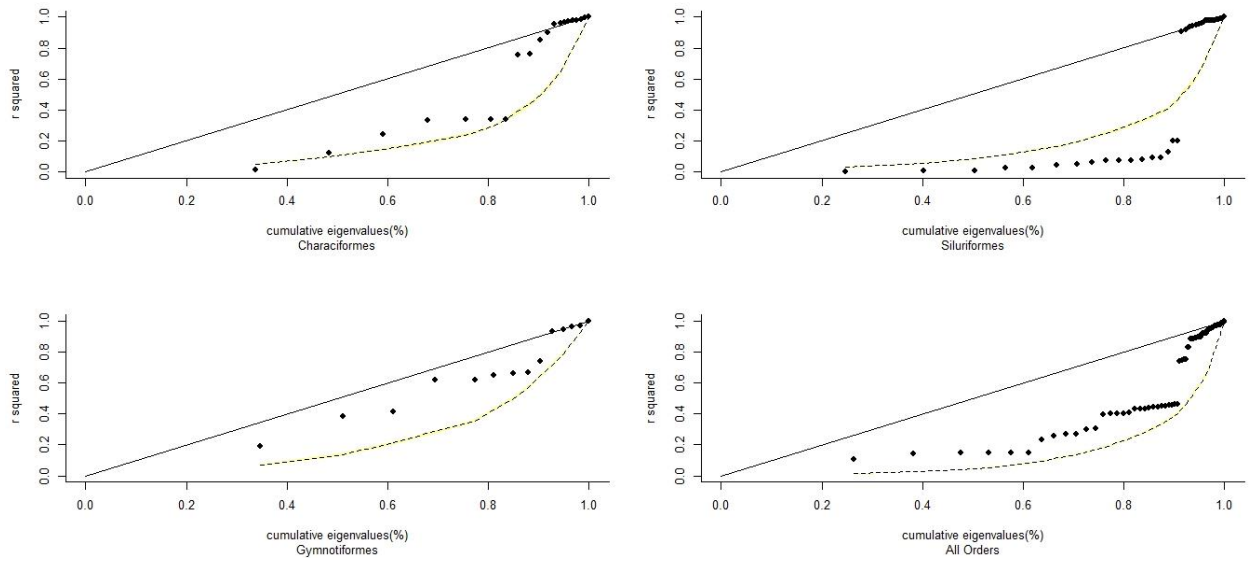


Figure 2: PSR curves for niche breadth values within each order (Characiformes, Siluriformes and Gymnotiformes) and for all orders together. The dots over the line indicate that for some species the traits have evolved according to Brownian model of evolution.

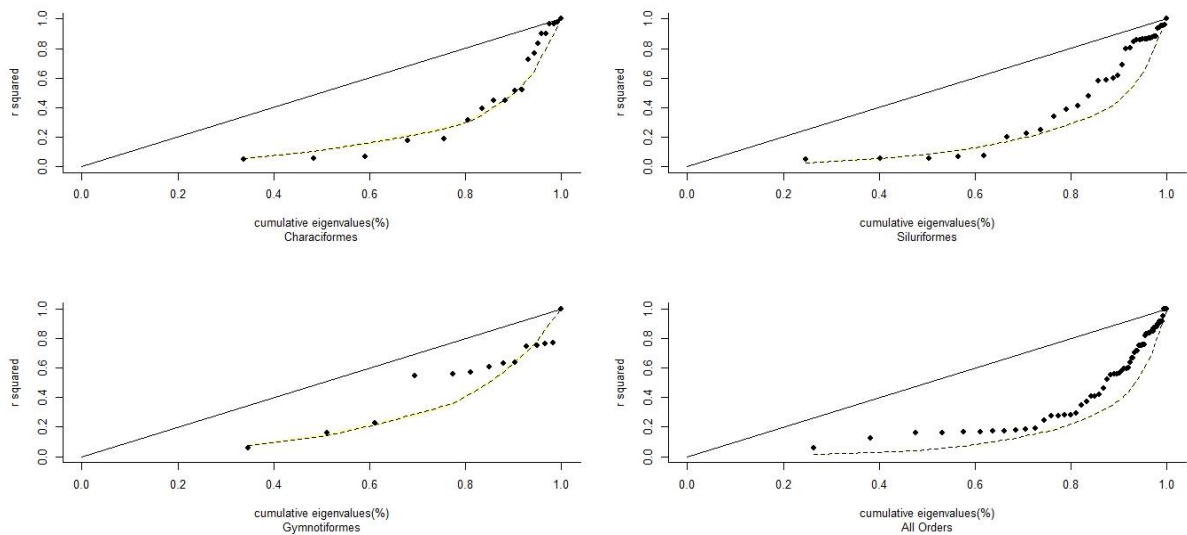


Figure 3: PSR curves for niche position values within each order (Characiformes, Siluriformes and Gymnotiformes) and for all orders together. The dots over the line indicate that for some species the traits have evolved according to Brownian model of evolution.

Discussion

Our findings showed the existence of phylogenetic structure in species' niche properties among taxonomic orders, but no significant phylogenetic pattern within individual orders. Accordingly, and despite the low values for global Moran's I and PVR, our results suggest niche conservatism among orders. However, we did not find support for niche conservatism when orders were analyzed individually. PSR show slow niche evolution both among and within orders, which could also indicate niche conservatism within orders.

The absence of phylogenetic signal in niche characteristics within the orders may be due to the scarcity of information about sister groups (i.e. closely related terminal taxa) in the phylogenies employed in this study. As our focus was on stream-dwelling fish species, and despite having a good representation of the main lineages for the taxonomic orders in the phylogenies, the scarcity of information regarding species pairs possibly impaired our capacity to detect niche conservatism within the orders. Moreover, the absence of temporal resolution of our phylogenies (i.e. calibrated branch lengths) may also explain the apparent absence of niche conservatism within the three orders. Niche conservatism in fishes was also analyzed by McNyset (2009) for 28 species from six clades of endemic freshwater fishes from North America. However, in that work she tested the niche conservatism with reciprocal predictions with ecological niche models, and in this study we used an evolutionary approach by phylogenetic signal to test phylogenetic niche conservatism.

The observed niche conservatism supposedly resulting from a slow rate of evolution may have some ecological consequences for conservation biology planning (Wiens *et al.*, 2010). The niche conservatism could limit species capability to adapt to new environmental conditions and lead to an extinction of such species facing climate change (Wiens & Graham, 2005; Wiens *et al.*, 2010). One of the major problems in relation to climate change in the

Amazon is the change in hydrologic cycles, resulting in stronger drought and floods affecting limnological and habitat conditions (Barletta *et al.*, 2010). The life cycles of Amazon fish species are strongly associated with the predictability of dry and rainy seasons, which is also observed among stream fishes that use temporary ponds for shelter, feeding and reproduction in rainy season (Espírito-Santo *et al.*, 2013). In this sense, the observed niche conservatism suggests that the expected climate changes may negatively affect several species simultaneously, resulting in biodiversity loss and potentially compromising ecological functions and services in stream systems.

Some fish species from *terra-firme* streams are associated with certain habitat characteristics (as noted above), and the observed high turnover of species among streams seems to be associated to a limited capacity to disperse (Mendonça *et al.*, 2005; Albert *et al.*, 2011a). Despite such dispersal limitations there are many widespread species shared among sub-basins (Albert *et al.*, 2011a), which could be due to the dynamic of capture and re-capture of drainages by adjacent basins, and to headwater connections (BurrIDGE *et al.*, 2006).

In plain rivers like the Amazon it is common the occurrence of some changes in drainage, as headwater stream capture or geodispersal that mix and split the pool of species (Albert & Reis, 2011c). River capture is an important process for allopatric speciation and range expansion in freshwater fishes, especially for taxa with limited dispersion ability (BurrIDGE *et al.*, 2006; Winemiller, López-Fernández, *et al.*, 2008). The current Amazon landscape started to assume its modern configuration in the Paleocene, about 60 Mya, with the uplift of central Andean Cordillera, and acquired its configuration in upper Miocene/earlier Pliocene, about 5 Mya (Hoorn *et al.*, 2010; Albert & Reis, 2011c). During this process the Amazon basin was subjected to dramatic modifications in its landscape, which led ultimately to an increase in the regional fish species diversity. One hypothesis for

this high species richness was presented by Albert and collaborators (2005) who state that the evolution of freshwater clades in the Amazon is a combination of a long time for speciation, low extinction rates, immigration and ecological opportunity. A similar hypothesis was placed by Winemiller and collaborators (2008) which states that the Guiana and Brazilian Shields may have preserved a large portion of the regional fish diversity during the marine incursions, leading to less strong species loss compared to other continents, such as Asia.

Other studies explain the high species richness of tropical regions as a consequence of niche conservatism, a hypothesis known as Tropical Niche Conservatism (Wiens & Donoghue 2004). This hypothesis states that tropical regions had enough time and area to allow species evolution, that most species had its origin in the tropics, and that only few species have been able to colonize temperate regions (Wiens & Donoghue 2004; Giehl & Jarenkow, 2012). Cooper and collaborators (2011) found higher niche conservatism among tropical mammal species with small body and range size, assigning it to the higher climatic homogeneity observed in the tropics.

Characiformes, Siluriformes and Gymnotiformes are early occupants of the freshwater systems in the Neotropical region, along with some ancient groups such as Osteoglossiformes and Lepidosireniformes (Albert & Reis, 2011c). There are Characiformes and Siluriformes fossils assigned to modern genera and subfamilies at least since the Paleogene (Albert *et al.*, 2011b). It is also known that the electric eels of the genus *Gymnotus* (Gymnotiformes) have its origins before the Andes uplift, with four trans-Andean groups (Albert *et al.*, 2011a). This niche conservatism pattern for old groups was also found among anurans. Hof and collaborators (2010) tested the niche variance among hierarchical levels of phylogeny and found higher values above family level, suggesting a relation with a climatic constancy since the Cretaceous. Similar results were shown by Olalla-Tárraga and collaborators (2011)

comparing the level of niche conservatism between amphibians and mammals, evidencing stronger niche conservatism in the older group, the Amphibians.

Rates of climatic niche evolution are associated to species' physiological features (e.g. if a clade or species can tolerate changes in temperature and altitude); and can affect the ability to disperse from tropical to temperate regions (Kozak & Wiens, 2010). Some authors consider two filters operating in the evolution of a community assembly. One of them is the physiological requirements of the species (normally climatic niche, or as called β niche), and once they "pass" through this physiological filter it evolves as a conservative force. The other filter is composed by local requirements that allow the coexistence of congeneric species, α niche (Silvertown *et al.*, 2006a,b). These authors found absence of phylogenetic signal in the structure of the communities, suggesting that β niche evolves slowly, affected by niche conservatism, whereas α niche would evolve faster (see Silvertown *et al.*, 2006b for β and α niche details). According to these authors areas with high species richness normally have conservative β niche, allowing the occurrence of congeneric species. We did not test if there are differences in niche conservatism between α and β niches, but the seemingly absence of phylogenetic signal in our results suggests that the coexistence of Amazon stream fishes may be related to α niche characteristics.

The three taxonomic orders included in this study are very different in terms of morphology, behavior and ecological requirements. In general, Characiformes are diurnal fishes that occupy mainly the mid and upper layers of the water column; Siluriformes (naked and armored catfishes) are mostly nocturnal and benthic, and Gymnotiformes (electric knifefishes) are also nocturnal and nektobenthic (Nelson, 2006), and such characteristics could allow them to live in sympatry. However, morphological differences among closely related species are expected to be considerably smaller, also influenced by NC. In this sense,

it is remarkable that 11 species of the electric knifefish *Gymnotus* can be found in simpatry in the western Amazon (Albert *et al.*, 2005).

Amazon's upland forest streams present high habitat heterogeneity, but its availability (e.g. temporary ponds along the stream channel) for the fish fauna may be influenced by the seasonal rainfall, which can affect fish movements. Espírito-Santo and collaborators (2013) recently showed that in central Brazilian Amazon, some fish species move from the stream channel to marginal ponds in the rainy season, and such movements can be explained by their life-story strategies (mainly reproductive tactics). Our findings, may suggest the geomorphology of rivers in the Amazon could have led to the current species' general distribution patterns, but stream fishes are affected by local habitat requirements under an unchanged Grinnellian niche. Despite of its old age, the modern freshwater *terra-firme* stream fish fauna was assembled after the Amazon basin has acquired its modern configuration. Thus, the Grinnellian niches that we witness today may reflect the overall environmental stability of the tropical region and not be informative about the clade evolution. This niche stability and niche conservatism in Amazon stream fishes could increase the extinction risk of stream fish species in face of anthropic impacts. As stated above, climatic niche conservatism could lead to local species extirpation – or extinction - under global climate changes (Wiens & Graham, 2005; Cooper *et al.*, 2011) and other anthropogenic impacts, such as deforestation and dam construction.

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Supplementary S1

Table 1: Literature Phylogenetic data used in this study about species of Characiformes, Siluriformes and Gymnotiformes.

Order	Phylogenies
Characiformes	Abe et al. 2013
	Ortí et al. 2008
	Sidlauskas and Vari 2008
	Pretti et al. 2009
	Mirande 2010
	Calcagnotto et al., 2005
Siluriformes	Sullivan et al., 2006
	Pinna et al., 2007
	Cramer et al., 2011
	Chiachio et al., 2008
	Armbruster 2004
Gymnotiformes	Lovejoy et al. 2010
	Maldonado-Ocampo et al. 2014
	Albert et al. 2005

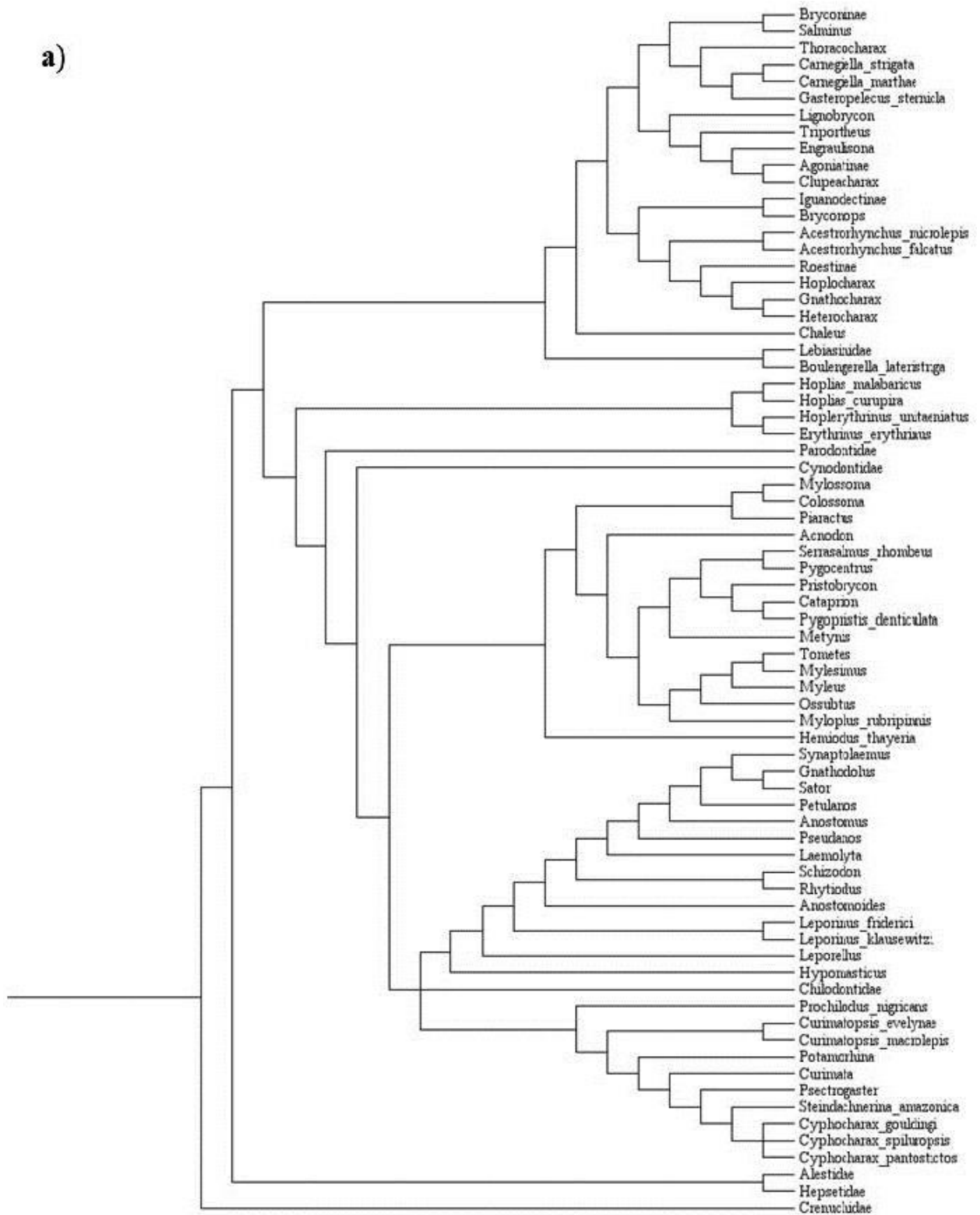
Table 2: Outlying mean index and niche breadth values for all orders and species analyzed

Orders	Species	OMI	breadth
Characiformes	<i>Acestrorhynchus falcatus</i>	0.170	1.128
	<i>Acestrorhynchus microlepis</i>	0.209	1.547
	<i>Boulengerella lateristriga</i>	3.546	0.360
	<i>Carnegiella marthae</i>	2.912	0.880
	<i>Carnegiella strigata</i>	2.141	0.817

	<i>Curimatopsis evelynae</i>	2.977	0.633
	<i>Curimatopsis macrolepis</i>	1.726	1.763
	<i>Cyphocharax gouldingi</i>	1.002	1.032
	<i>Cyphocharax spiluroopsis</i>	0.899	2.311
	<i>Erythrinus erythrinus</i>	0.965	1.863
	<i>Gasteropelecus sternicla</i>	1.420	5.304
	<i>Hemiodus thayeria</i>	3.940	3.614
	<i>Hoplerythrinus unitaeniatus</i>	0.100	0.977
	<i>Hoplias curupira</i>	0.727	4.420
	<i>Leporinus friderici</i>	0.251	2.917
	<i>Hoplias malabaricus</i>	0.031	0.742
	<i>Leporinus klausewitzii</i>	5.506	0.570
	<i>Myloplus rubripinnis</i>	3.453	17.395
	<i>Prochilodus nigricans</i>	0.269	4.899
	<i>Serrasalmus rhombeus</i>	0.255	1.802
	<i>Steindachnerina amazonica</i>	1.782	0.969
Siluriformes	<i>Acanthodoras cataphractus</i>	0.805	2.186
	<i>Acestridium gymnogaster</i>	1.742	0.138
	<i>Acestridium martini</i>	3.544	0.176
	<i>Acestridium discus</i>	3.841	0.562
	<i>Auchenipterichthys punctatus</i>	2.325	0.298
	<i>Bunocephalus coracoideus</i>	0.737	1.074
	<i>Bunocephalus verrucosus</i>	3.188	0.982
	<i>Callichthys callichthys</i>	0.086	0.809
	<i>Corydoras elegans</i>	1.631	0.460
	<i>Coydoras julii</i>	2.292	1.594
	<i>Denticetopsis seducta</i>	0.558	0.681
	<i>Farlowella platorynchus</i>	2.126	0.942
	<i>Farlowella smithi</i>	2.067	1.503
	<i>Gladioglanis conquistador</i>	1.708	0.728
	<i>Helogenes marmoratus</i>	1.052	1.771
	<i>Hypostomus cochliodon</i>	6.222	2.796
	<i>Imparfinis pristos</i>	0.880	1.691
	<i>Imparfinis stictonotus</i>	2.696	1.541
	<i>Ituglanis amazonicus</i>	0.433	0.878
	<i>Megalechis picta</i>	0.351	0.484
	<i>Myoglanis koepckeii</i>	3.383	0.693
	<i>Otocinclus mura</i>	1.070	1.078
	<i>Otocinclus caxarari</i>	1.285	0.461
	<i>Otocinclus hoppei</i>	1.751	1.219
	<i>Otocinclus vitatus</i>	5.624	2.750
	<i>Parotocinclus longirostris</i>	3.567	3.845
	<i>Physopyxis ananas</i>	2.056	0.273
	<i>Physopyxis lyra</i>	1.811	2.260
	<i>Rineloricaria lanceolata</i>	0.735	3.428

	<i>Scoloplax distolothrix</i>	6.236	13.645
	<i>Stauroglanis gouldingi</i>	8.034	1.285
	<i>Tatia brunnea</i>	2.849	2.272
	<i>Tatia gyrina</i>	3.418	0.185
	<i>Tatia intermedia</i>	0.947	1.349
	<i>Trachelyopterus galeatus</i>	3.863	3.745
	<i>Trachelyopterichthys taeniatus</i>	1.930	0.855
	<i>Trichomycterus hasemani</i>	2.170	0.597
Gymnotiformes	<i>Brachyhypopomus beebei</i>	0.590	1.252
	<i>Brachyhypopomus bevirostris</i>	1.437	1.702
	<i>Electroforus electrus</i>	0.758	2.001
	<i>Gymnotus coatesi</i>	1.642	0.564
	<i>Gymnotus carapo</i>	0.902	3.869
	<i>Gymnotus pendanopterus</i>	4.050	1.741
	<i>Gymnorhamphichthys petiti</i>	0.647	1.233
	<i>Hypopygus hoedemani</i>	1.900	0.208
	<i>Hypopygus lepturus</i>	0.251	1.336
	<i>Hypopygus neblinae</i>	1.752	0.644
	<i>Microsternarchus bilineatus</i>	0.780	0.851
	<i>Rhamphichthys marmoratus</i>	1.264	3.748
	<i>Steatogenys duidae</i>	1.232	0.875
	<i>Sternopygus castroi</i>	2.304	1.967
	<i>Sternopygus macrurus</i>	0.253	3.091

a)



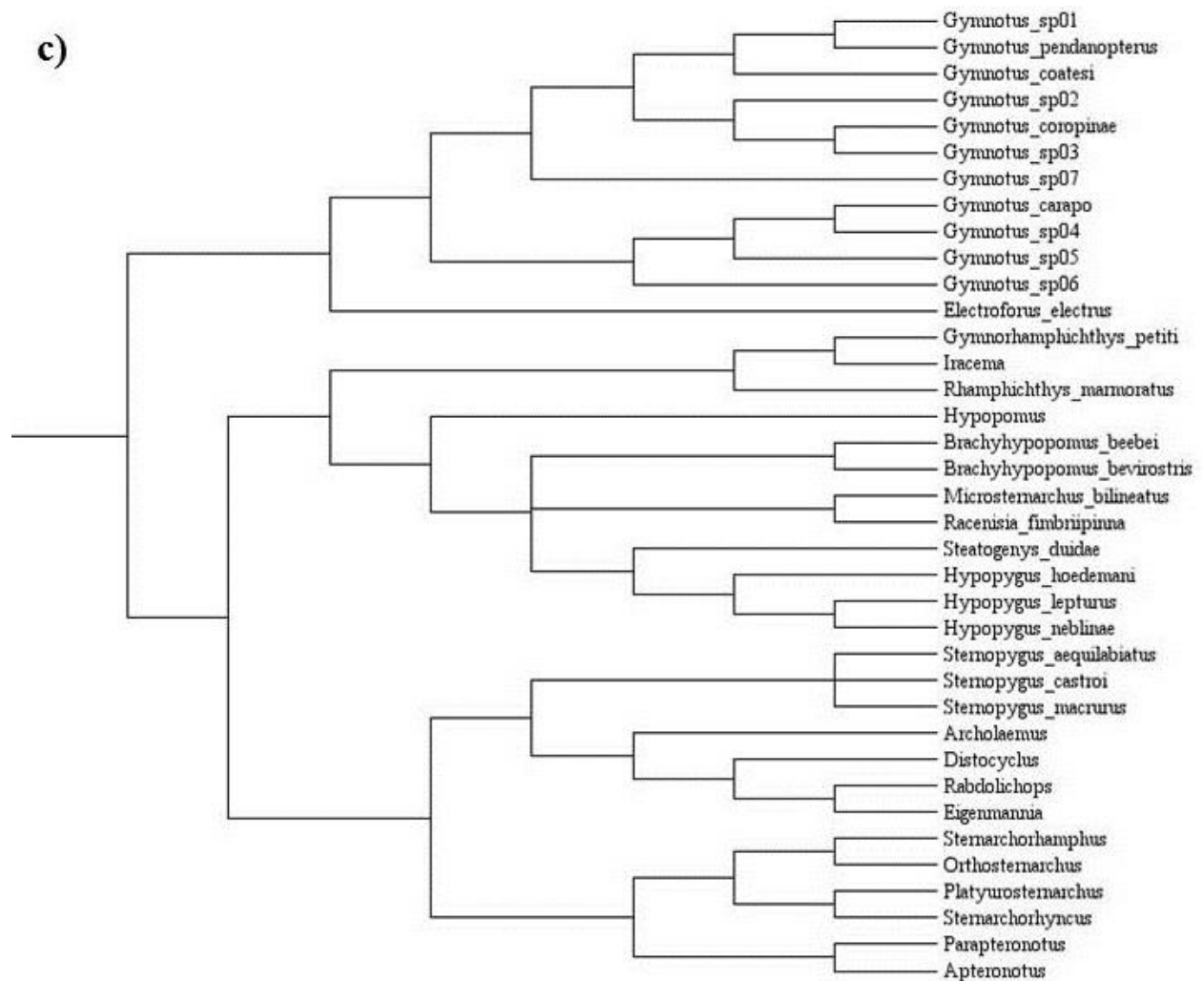


Figure 1: Assembled phylogenetic tree of Characiformes (a), Siluriformes (b) and Gymnotiformes (c).

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Capítulo 3

Amazon protected areas: Are Megareserves protecting the Amazon streams fishes?

Manuscrito em preparação para *Diversity and Distributions*

Are Megareserves protecting the Amazon's forest stream fishes?

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Abstract

Aim

Very large protected areas (i.e. Megareserves) were proposed to safeguard as much as possible of Amazon's biodiversity, both in terrestrial and aquatic ecosystems. Despite this purpose, these conservation units were created based on information derived from terrestrial

ecosystems and organisms. Thus, the aim of this study is to investigate whether these Amazon protected areas are being effective in conserving Amazon freshwater stream fishes.

Location

Brazilian Amazon.

Methods

We built potential species distribution models for 201 species of “*terra-firme*” stream fish. Gap and Prioritization analyses were conducted under three scenarios of increasing protection in the Brazilian Amazon: 1) considering only Integral Protection Areas (IPAs); 2) IPAs + Sustainable Use Areas (SUAs); and 3) IPAs + SUAs + Indigenous Territories (ITs). To perform such analyses we employed the results of previously generated species distribution models. We then compared the results of Gap and Prioritization analyses to a null model based on the protection provided by areas selected at random across the landscape.

Results

Widespread species represented by many occurrence points generally had lower values of area under curve and true skill statistics, which could be expected for large and spatially heterogeneous regions such as the Amazon. The Gap analysis did not reveal species with complete protection gaps (i.e. completely unprotected), but only partial gaps where at least 10% of their distribution range was included in protected areas. Nevertheless, most of these species were composed by wide-ranging species. Moreover, most of the official conservation units in the Brazilian Amazon do not include the priority areas for freshwater fish species conservation.

Main conclusions

Brazilian Amazon's megareserves, which were created aiming to conserve terrestrial ecosystems and organisms, are inadequate for conservation of freshwater stream fishes. It is strongly suggested that freshwater species and ecosystems should be considered as priorities for conservation and included in Systematic Conservation Planning initiatives in Brazil.

Keyword: Gap analysis, modelling, spatial prioritization, stream fishes, systematic conservation planning.

Introduction

Protected areas (PAs) are designed for protection and conservation of all components of the biodiversity, including populations, species, and ecosystems services, trying to isolate these elements from the threatening processes (MARGULES; PRESSEY, 2000). In order to make conservation areas more feasible to reach its conservation goals, Margules & Pressey (2000) proposed the Systematic Conservation Planning (SCP) approach. Since the SCP was created to optimize the protected areas, namely, maintaining natural processes and viable populations with the smaller possible costs, the principle of complementarity rather than richness have become crucial for the selection of target areas for conservation (see Justus and Sarkar, 2002 for details). The complementarity principle in a network of PAs is to choose areas that complement each other in relation to its biodiversity contents. Namely, if a given set of species and environmental characteristics are already present in a PA, the next area to be chosen must have different biodiversity components (JUSTUS; SARKAR, 2002).

Considering that one of the main SCP purposes is to optimize the limited funding for PAs,

the complementarity principle has increasingly being incorporated in conservation efforts (JUSTUS; SARKAR, 2002; RODRIGUES et al., 2003).

Environmental niche models (ENM) also constitute a powerful tool for SCP, especially to address the lack of information about species distribution (ARAÚJO et al., 2005; DINIZ-FILHO et al., 2009; STRECKER et al., 2011), providing information of suitable areas for species occurrence (JIMÉNEZ-VALVERDE; LOBO, 2007). This method became important and useful in areas with large gaps of information on species distribution, especially in tropical and developing countries where there is a direct competition for areas by farmers and conservationists, and scarce funding for conservation, such as in Brazil (NÓBREGA; DE MARCO JR., 2011). Mapping areas of potential occurrence of taxa could also be used in Gap analysis to evidence unprotected species under a network set of PAs (DINIZ-FILHO et al., 2009; NÓBREGA; DE MARCO JR., 2011). This may also be used to highlight priority areas for conservation (MOILANEN, 2005, 2012).

In 2000, Brazil has established the *Sistema Nacional de Unidades de Conservação da Natureza* (SNUC - National System of Conservation Units, LEI No 9.985, DE 18 DE JULHO DE 2000). SNUC establishes the Brazilian standards for creation, implementation and management of protected areas. According to SNUC, there are two categories of Protected Areas in Brazil: Integral Protection and Sustainable Use; later, the network of Indigenous Territories was incorporated to the National Protected Areas system. In 2003, the Brazilian government created the *Programa Áreas Protegidas da Amazônia* (ARPA – Amazon Protected Areas Program); since then, about 63 conservation units have been created in the Amazon. The conservation units in the Amazon are the largest protected areas in Brazil, with approximately 43% of the region's territory under government protection (VERÍSSIMO et al., 2011a). More than 50% of these new PAs in the Amazon were created between 2003 to

2010 in areas highly vulnerable to anthropogenic pressure, aiming to decrease the deforestation rates (VERÍSSIMO et al., 2011b).

Despite all the advances regarding preservation of the Brazilian Amazon, which have resulted in decreasing deforestation and carbon emission rates, little attention has been given to the management of its freshwater ecosystems (CASTELLO et al., 2013). Freshwater systems are arranged in dendritic networks, a trait that renders these ecosystems highly vulnerable, both in terms of local impacts (directly into rivers and streams), and of large-scale impacts in the surrounding terrestrial ecosystem (CASTELLO et al., 2013). Despite the vulnerability of freshwater ecosystems, the planning and management of water resources is still unsatisfactory in Brazil. In general, the priority areas for conservation are chosen targeting terrestrial organisms and ecosystems, and few studies take into account freshwater ecosystems as its main conservation goals (BROOKS et al., 2006). This could be due to the complexity surrounding conservation planning, and including freshwater biodiversity makes these efforts even more complicated (ABELL, 2002). Some authors believe that large protected “terrestrial” areas naturally encompass the freshwater ecosystems and could be considered surrogates for conservation of the inland aquatic biodiversity (PERES; TERBORGH, 1995; PERES, 2005). According to Peres (2005), conservation areas should be large enough to cover a number of wide-ranging terrestrial and aquatic species, and also considering large predators that need large areas to keep viable populations. This surrogacy could be in part true and was nicknamed by Amis and collaborators (2009) as “*incidental integration*”; by the way, the opposite could also be true, protecting large catchments could lead to a conservation of associated terrestrial organisms.

The Neotropical region comprises approximately 13% of freshwater vertebrate biodiversity in the world (AGOSTINHO; THOMAZ; GOMES, 2005). Currently, freshwater

fishes figure among the most threatened vertebrates in Brazil, due to continued habitat loss of these organisms associated to a lack of knowledge about the species' distributions and habitat requirements (NOGUEIRA et al., 2010). The Amazon Basin comprises approximately 7 million km² and harbors the highest freshwater fish species richness of the world, and 70% of this basin are located in Brazil (ABELL et al., 2008; GOULDING; BARTHEM; FERREIRA, 2003). Most of the knowledge about the Amazon fish fauna refers to commercial species that dwell in rivers and lakes. However, under pristine forest there is a dense hydrological network of first- and second-order upland streams, called *igarapés de terra firme*, harboring a diverse and poorly known fish fauna.

Bearing in mind all the efforts taken to protect the Amazon ecosystems, we addressed the question: Are these huge areas or Megareserves (*sensu* Peres, 2005) protecting the Amazon's stream fishes? The main aim of this work is to investigate if these large Amazon protected areas can be used as surrogates for conserving stream-dwelling fishes.

Methods

Data

The main database used in this study was obtained from Igarapés Project (www.igarapes.bio.br). The database includes approximately 400 sampling locations that represent 1st to 3rd-order *terra-firme* streams distributed throughout the Brazilian Amazon. Approximately 450 fish species are included in the database and were sampled using standardised methodology and collecting effort (see Mendonça *et al*, 2005 for details). These small upland forest streams are not influenced by the seasonal flood pulse and lateral expansion of the main rivers and lakes. Instead, these streams are subjected to short-term

(hour to a few days) flooding after strong rainfall, which occurs more frequently during the rainy season that ranges from December to May in Central Brazilian Amazon.

We started our analyses with the species-occurrence points included in the Igarapés Project database. We chose only species with no taxonomic uncertainties, present at least in five occurrence points. Additionally, we looked for information on those species' occurrences in the Species Link website (<http://splink.cria.org.br/>). This resulted in 201 species, with 111 Characiformes, 4 Cyprinodontiformes, 15 Gymnotiformes, 19 Perciformes, 50 Siluriformes, and 2 Synbranchiformes. Both databased summed 7999 occurrence points of forest stream fishes in the Brazilian Amazon.

A set of environmental variables was chosen based on the intrinsic collinearity of many limnological, macro-climatic and macro-topographical variables, in order to obtain the best set of environmental layers to model the distribution of Amazon stream fishes (Frederico et al, submitted manuscript). The climatic macroscale variables were obtained from WorldClim (www.worldclim.org): annual mean precipitation (AMP), annual mean temperature (AMT), seasonality of precipitation (SP) and seasonality of temperature (ST). We also used geomorphological variables which are correlated with the amount of nutrients and suspended sediments in streams and rivers (ANGERMEIER; KARR, 1983; GOULDING; BARTHEM; FERREIRA, 2003; SIOLI, 1985). Information about terrain slope, flow accumulation and river orders are variables that reflect the flow and size of streams, and were obtained from Hydro1k a hydrological database (www.usgs.gov). Soil type characteristics were gathered from Food and Agriculture Organization of the United Nation's database (www.fao.org.br). All descriptor variables were obtained for pixels of 4x4 km of resolution.

Models

For modelling species distributions we used MaxEnt algorithm using “dismo” package in R software (R Development Core Team 2012). This algorithm works with the presence of the species (occurrence points) and categorical variables. Additionally, this method was chosen because it has a good performance even when few occurrence points are available for analysis (NÓBREGA; DE MARCO JR., 2011). MaxEnt estimates the environmental suitability by fitting a function close to the uniform distribution under the environmental information associated to the occurrence points (PHILLIPS; ANDERSON; SCHAPIRE, 2006). This method can discriminate between the environmental variables associated to the occurrence data and the background variation of the predictor variables based on 10000 random points of the background information (PHILLIPS; DUDÍK, 2008).

Model evaluation was performed using the Area the Under Curve (AUC), which is a threshold-independent measure commonly used (FIELDING; BELL, 1997). This measure could be interpreted as an average true positives values (sensitivity) of all possible false positive values (specificity), producing a global measure of fit for the model. These values are then plotted (sensitivity against 1-specificity) to generate what is known as the ROC (Receiver Operating Characteristic) curve (Fielding & Bell, 1997). However, the AUC could be subjected to problems related to the use of prevalence in the model (LOBO; JIMÉNEZ-VALVERDE; REAL, 2008).

The True Skill Statistics (TSS) is threshold-dependent and less sensitive to prevalence, representing the average rate of prediction success expressed as values varying between -1 and 1 (LIU; WHITE; NEWELL, 2009). It is important to highlight that our approach was based on presence data only (not including information on the local abundance of the targeted species), and for deriving presence/absence information from these models is necessary to determine thresholds. We used the Minimum Difference Threshold Criterion

(MDT) that are expected to minimise omission and commission errors (JIMÉNEZ-VALVERDE; LOBO, 2007). TSS and AUC were calculated using background data as pseudo-absence, which is a common procedure in recent SDM literature (Liu *et al.*, 2009).

Gap Analysis

Gap Analysis allows to evaluate how well the targeted species are represented in Protected Areas (PAs) by comparing the distribution of species and/or environmental characteristics with the distribution of conservation areas (JENNINGS, 2000; RODRIGUES *et al.*, 2003). We used the suitable areas (ENM results) for fish species occurrence to represent the species' distribution areas used in the GAP analysis. The maps (shapefiles) of officially protected areas by federal laws in the Brazilian Amazon were obtained from *Ministério de Meio Ambiente* – MMA (Brazilian Environment Ministry; <http://www.mma.gov.br/areas-protegidas>). Brazil's Federal Protected areas are divided into two categories. (1) Integral Protection Areas (IPA), where only scientific research is allowed and, in some cases, touristic activities (i.e. in National Parks), but no resource extraction nor the presence of human populations. (2) Sustainable Use Areas (SUA), where it is possible to perform resource extraction but only based on sustainable management strategies; traditional populations are allowed to live into these areas and make use of some of its natural resources. Indigenous territories (IT) are federal areas where indigenous populations have the possession and usage rights, according to Brazil's Federal Constitution from 1988.

We ran the analysis considering three scenarios of different protection levels: (1) Integral Protection Areas only (IPA); (2) IPA plus Sustainable Use Areas (SUA); and (3) IPA+SUA + Indigenous Territories. Under these scenarios the species were classified according the size of their distribution, in Protected (P), when the target range size is entirely

included into PAs, Partial Gap (PG), when just a portion of the occurrence range size is included into PAs; and Gap (G) when the target species' distribution range is completely outside the PAs (see Rodrigues et al, 2003, for details). The target protected size varies in relation to species range size. Small range size species ($< 1.000\text{km}^2$) should have 100% of their distribution into PAs, and widespread species (above 250.000km^2) should have at least 10% of their ranges into PAs to reach the targeted protection. Following Rodrigues et al (2003), for species with intermediate ranges the target was interpolated using a logarithm transformation between those extremes.

Zonation

We also used the spatial prioritization software Zonation (MOILANEN, 2005) to indicate the main areas for conservation of the targeted freshwater stream fish species. The Zonation algorithm is based on the complementarity of biodiversity protection, and starts assuming that the whole area is protected; then, the software starts removing spatial cells according to its conservation value. As a removal rule we used the core-area, which keeps the best suitable area for the species, take into account all species, even if there is a cell where only one species is important. The input species layers were the results of the ENM model as explained above, and attributing equal weights to all species. It is important to highlight that most of the stream-dwelling species included in this study have not been evaluated according to the IUCN criteria, and for that reason we used equal species weight to perform the analysis. Since our objective is just to know the main areas for conservation of fish species, we did not use information on the threatened status of species nor PAs in our analysis.

Have been created based mainly on terrestrial biodiversity goals, we also tested Protected Areas' effectiveness for stream fish conservation by comparing them to areas created at random (pixels). We calculated the mean prioritization rank for pixels inside minus

the mean rank outside PAs, and tested it against the null hypothesis of equal ranks by a randomization test. We randomized the pixels of each PA category (IPA, IPA+SUA and IPA+SUA+IT) in relation to zonation prioritization rank pixel values, repeating the process 1000 times.

Results

Models

We built ENM for 201 species of Amazonian stream fish species. The AUC values varied between 0.783 and 0.997, for *Hoplias malabaricus* (Characiformes: Erythrinidae) and *Oxyropsis wrightiana* (Siluriformes: Loricariidae), respectively. *Hoplias malabaricus* is a widespread and common predatory species, and *Oxyropsis wrightiana* is a small-sized periphytivorous armored catfish which has smaller occurrence area. Widespread species with many occurrence points usually had lower AUC values (Table 1 S1). The TSS values were also low, varying between 0.000 and 0.153. *Pyrrhulina zigzag* and *Elachocharax pulcher* (Characiformes), and *Scoloplax distolothrix*, *Denticetopsis seducta* and *Megalechis picta* (Siluriformes) had the lowest TSS values and are typical stream-dwelling species, whereas *Oxyropsis wrightiana* had the highest value (Table 1 S1).

Gap Analysis

A Gap Analysis was performed with suitable areas (ENM results) for the 201 species of freshwater stream fishes (Table 1 S1). This analysis did not show any gap species, as all species had at least a portion of their distribution range included in PAs. Thus, we had only partial gap (with less than 10% of its suitable area into PAs) and protected (at least 10% of its

suitable area into PAs) species (Figure 1). Under the first scenario – the analysis performed only with integral protection areas (IPAs) – we found that there were no species under protection (Figure 1A), but only partial gap species (Figure 3A). Under the second scenario – adding both IPAs and Sustainable Use Areas – about 50% of the species were protected (Figure 1B), the target reaching almost 160%, but only for widespread species with range size usually above 250.000km² (Figure 1B). Nevertheless, they do not have more than 15% of their suitable area into PAs (Figure 2B). Finally, the last scenario protected more than 80% of the selected species and covered nearly 25% of the species' distributions, including some species with ranges lower than 250.000km² (Figure 1C). However, most species had about 20% of their range areas into PAs (Figure 2C).

Most species included in protected areas of any category have their potential range sizes higher than 250.000km², but even increasing the PAs cover (from scenario 1 to 3) the species with small range sizes were void of protection (Figure 3). In sum, the Brazilian Amazon's PAs are not effectively protecting the freshwater stream fishes. The observed increase in the percentage of protected species by adding non-integral PAs was just due to the increase in the analyzed area. Figure 4 shows the decrease of partial gap areas under the three different scenarios.

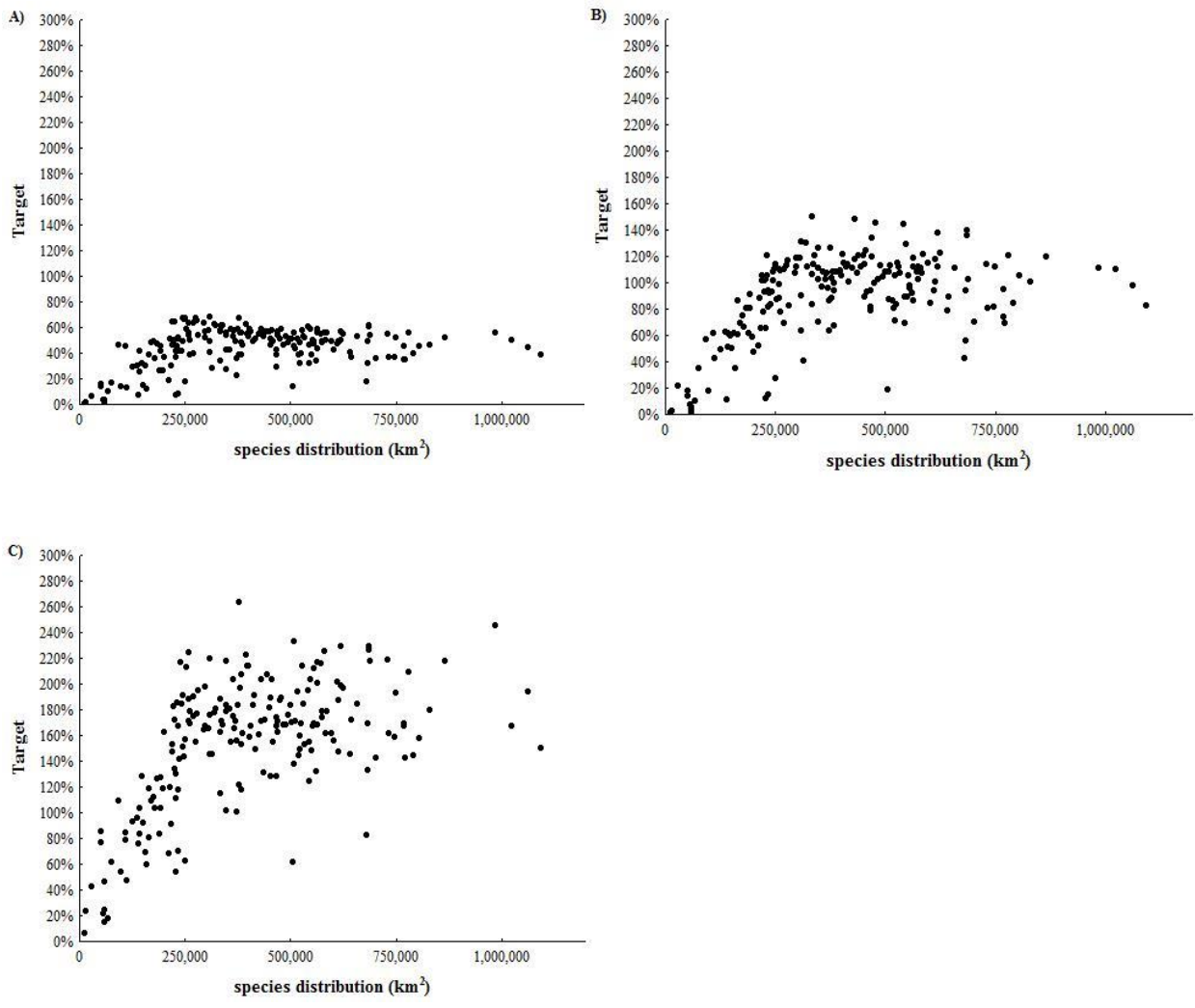


Figure 1: Species potential range size and proportion of targeted protection according to each scenario of PA. A) only IPA; B) IPA+SUA; C) IPA+SUA+IT.

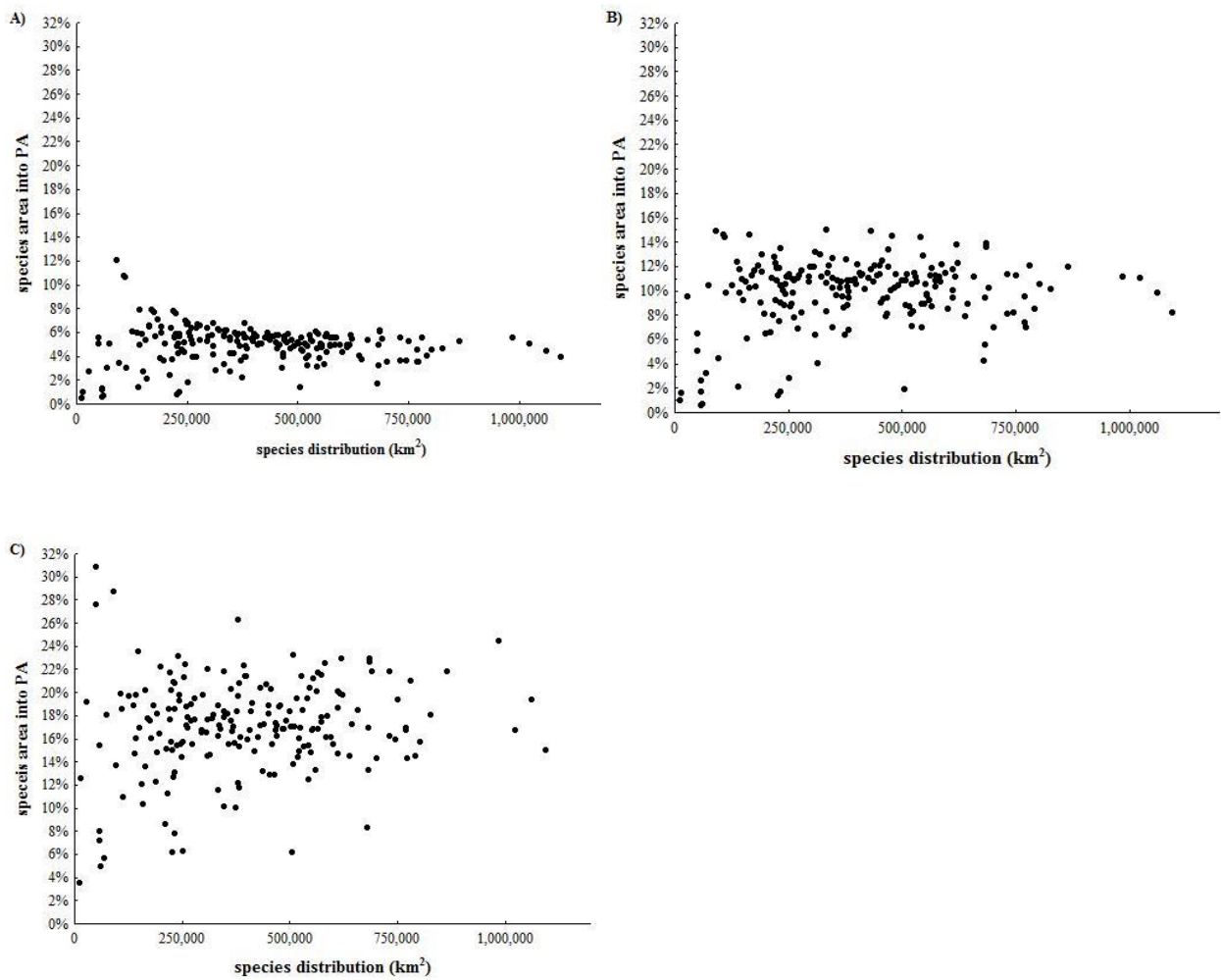


Figure 2: Proportion of species area into PAs according to their suitable range size. A) IPA;
 B) IPA+SUA; C) IPA+SUA+IT.

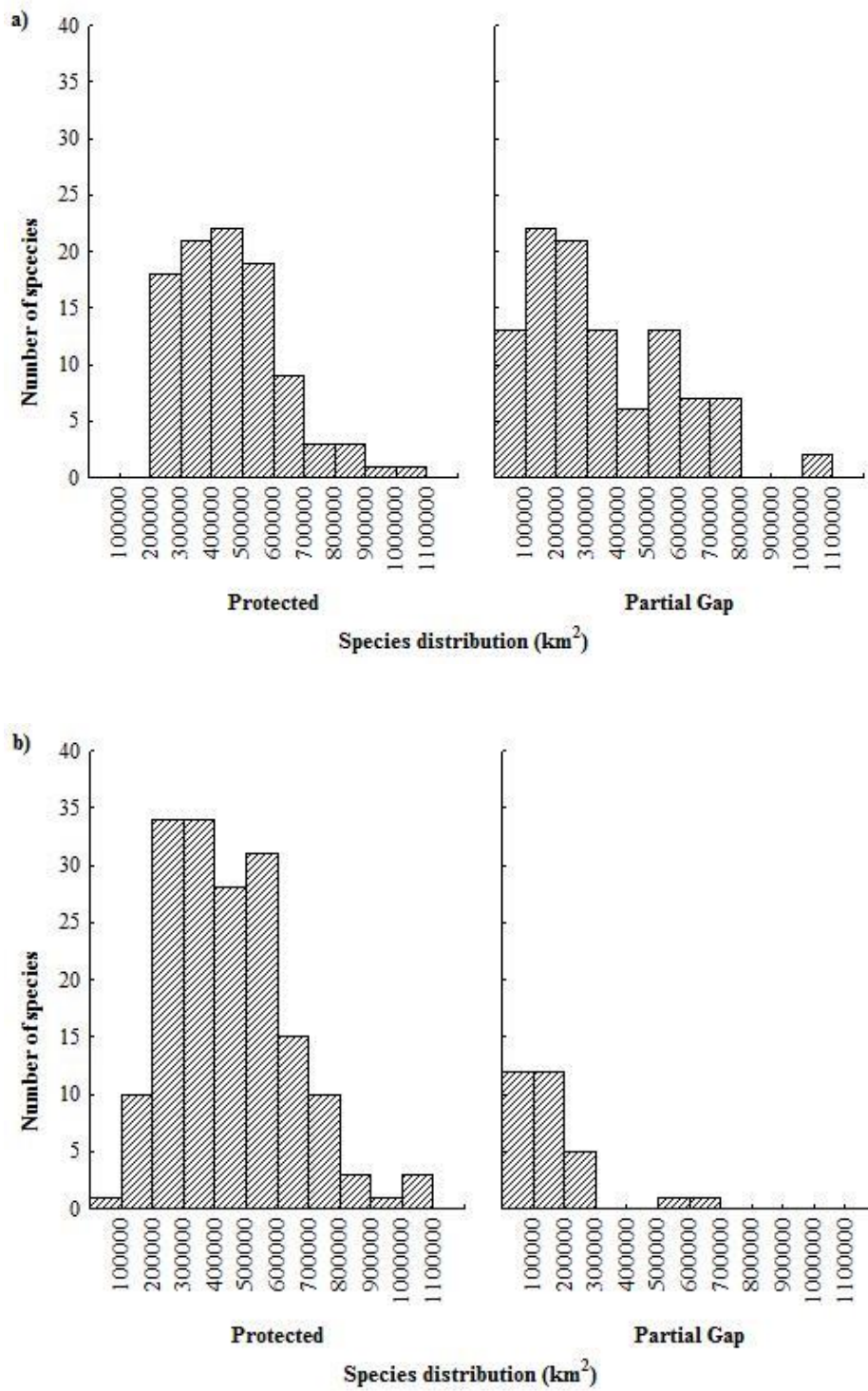


Figure 3: Classes of targets in relation to species' range size protected into PAs scenarios. A) IPA+SUA; B) IPA+SUA+IT.

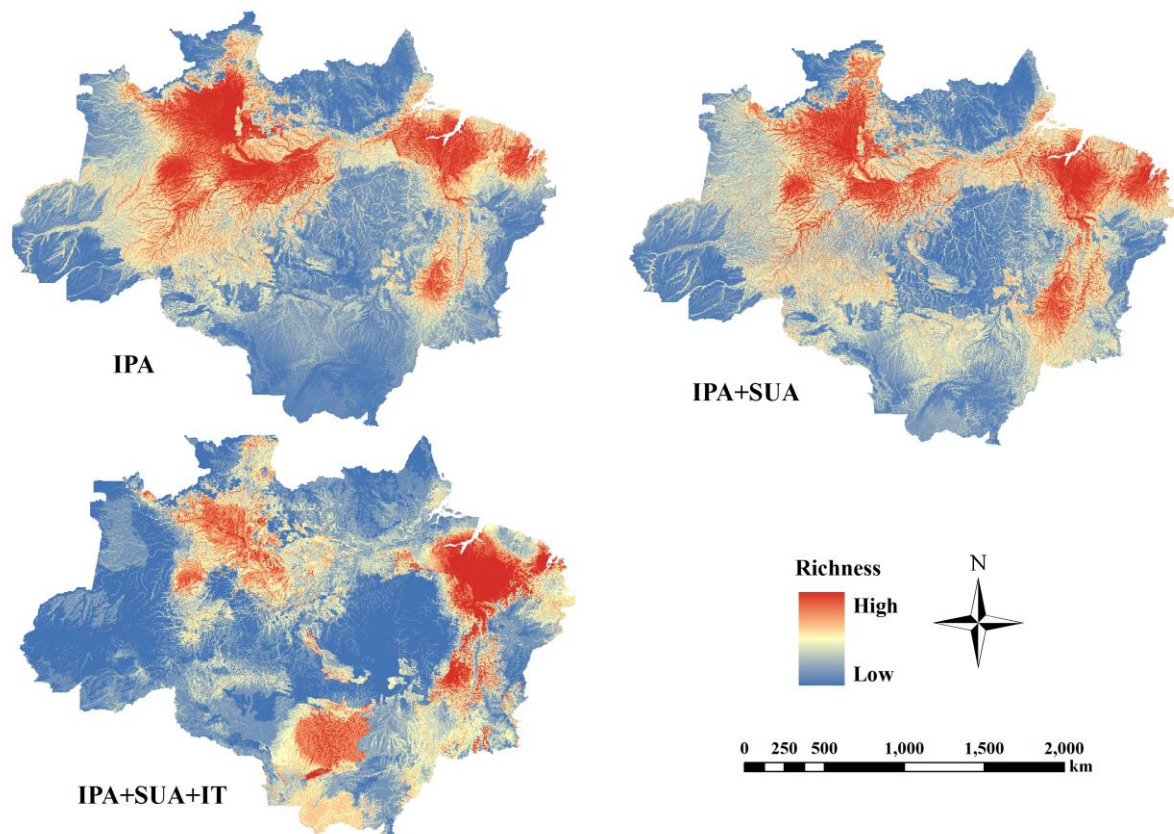


Figure 4: Map of Gap analysis for 201 species of stream fish species in the Brazilian Amazon. The richness of partial Gap freshwater stream fishes in each scenario. IPA, Integral Protection Area. SUA, Sustainable Use Area. IT, Indigenous Territory. Red areas indicate higher richness of partial gap species.

Spatial Prioritization

We plotted the PAs scenarios in Zonation map of rank areas (Figure 5). The red areas are the priority areas for conservation of stream fishes. The majority of current PAs are not in the red areas, especially the IPAs. There are 16 IPAs and 18 SUA conservation units covering the priority areas from a total of 61 IPAs and 18 SUAs, respectively. The best “protected areas” covering the proposed priority areas for stream fish conservation are the ITs (Figure

5). It is important to note that there is some overlap among PA categories, with six IPAs overlapping ITs.

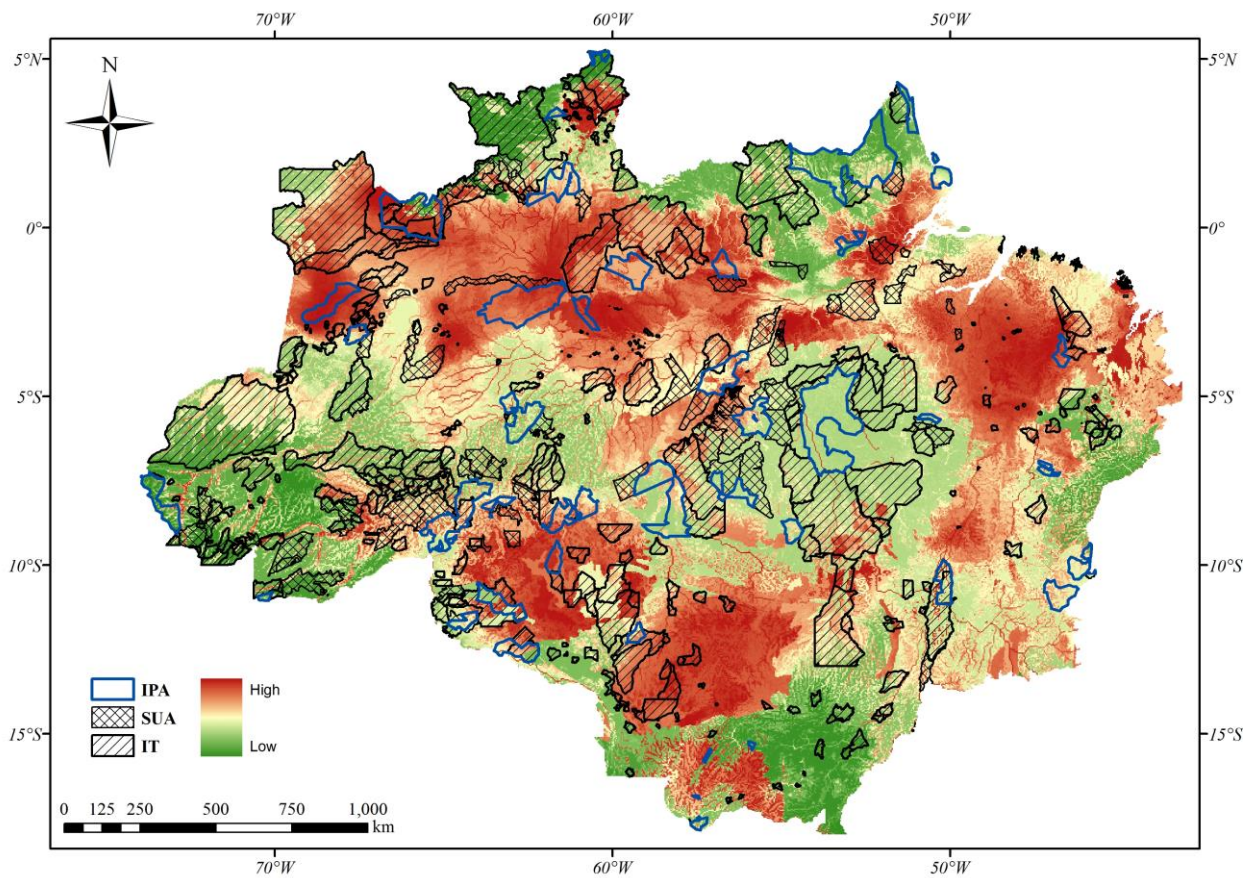
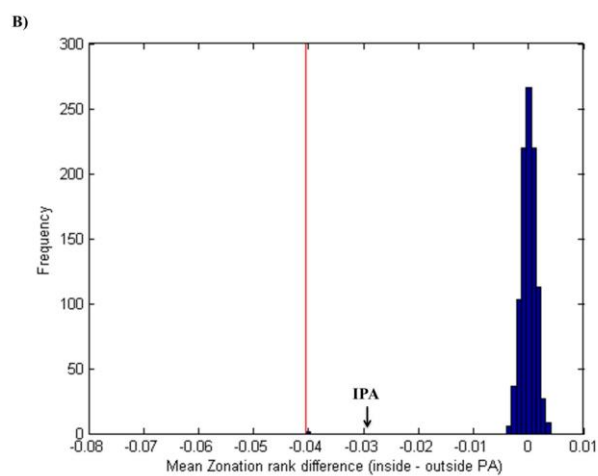
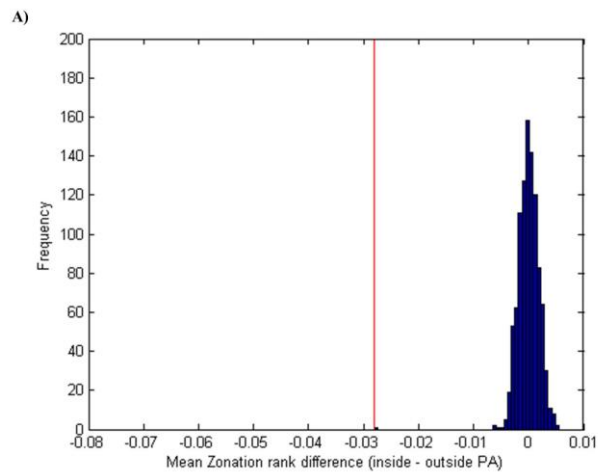


Figure 5: Map of the Brazilian Amazon delimiting the priority areas for stream fish conservation (colors) and federal protected areas (polygons). Red - highest priority areas. IPA - Integral Protection Area; SUA - Sustainable Use Area; IT - Indigenous Territory.

The result of the randomization test showed that despite the increase of PAs, they are not covering the priority areas for conservation of Amazon stream fishes. Considering only IPAs, the mean difference between rank prioritization values inside and outside them were - 0,03, indicating that priority areas are outside of this category of PAs (Figure 6A). When adding IPAs and SUAs the difference between priority areas inside and outside PAs

increased -0.04 in relation to the mean difference (Figure 6B). In the scenario with all categories of PAs (IPA+SUA+IT) the difference between rank prioritization values inside and outside PAs was even higher, -0.07 (Figure 6C). These increases in differences values show that the Amazon PAs are not effectively including the conservation priority areas for amazonian stream fish.



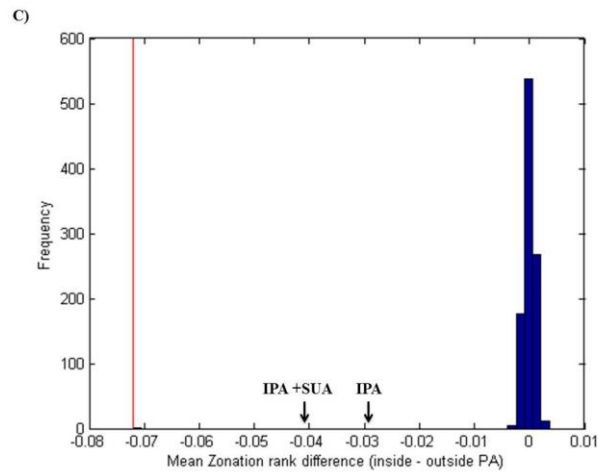


Figure 6: Zonation Mean rank values. The red line indicates the difference of mean observed values in relation to mean rank values into PAs. A - Integral Protection Areas (IPA). B - IPA + Sustainable Use Areas (SUA). C - IPA+SUA+ Indigenous Territories.

Discussion

Our findings demonstrate that the current system of Protected Areas in the Brazilian Amazon probably is not effectively protecting stream fishes. The Gap Analysis showed that, even increasing potential covering by the PAs (IPA+UPA+IT), species with low distribution ranges remain unprotected. Zonation rank priority areas are based on the complementarity principle (MOILANEN, 2005), and this approach points out to an even worse scenario. Our results are in agreement with Castello and collaborators (2013) that states that the Amazon PAs ignore river catchment areas, and fails to protect freshwater ecosystems from impacts of dams, pollution and deforestation. Thus, our prioritization analysis supports the need of a re-evaluation of the strategy to select areas to be officially protected in the Brazilian Amazon regarding the conservation of stream fishes. Also, we do not find any support to the claim that megareserves created on the basis of terrestrial organisms and landscapes could adequately

protect the different groups that compose the Amazon's biodiversity (PERES, 2005), especially the aquatic species.

Terrestrial and freshwater systematic planning normally considers these ecosystems separately. The problem of not including freshwater ecosystems in systematic conservation planning and/or prioritization areas is not exclusive to Brazil. National Parks Service (NPS) of the United States was also created mainly focusing on terrestrial organisms and ecosystems. Lawrence and collaborators (2011) found that 38% of native freshwater fish species in the US are uncovered by the PAs, more than a half of which are nationally imperiled and 80% of these are endemic. Endemic species generally have small range sizes, and our findings show that the unprotected species were predominantly composed by small range size species.

Beger and collaborators (2010) highlighted the idea of linking terrestrial and aquatic ecosystems in the process of Systematic Conservation Planning (SCP). In South Africa, Amis and collaborators (2009) compared the SCP for freshwater and terrestrial ecosystems separately, and then integrated both targets to show an efficient way to identify biodiversity priorities areas. They found that by using integrated targets (equal weights) for terrestrial and freshwater ecosystems resulted in smaller requirements for protected areas than for each ecosystem separately. Nevertheless, they also reinforced the importance of carrying out systematic planning analyses separately for ecosystems in order to reach their unique requirements.

A SCP produced for freshwater ecosystems in the western Amazon, in Madre de Dios River basin was carried out by Thieme and collaborators (2007). Due to the lack of information on freshwater species, they performed a gap analysis using freshwater habitat types to classify sub-basins, streams and floodplains. In that study the authors had access to

finer information about hydrologic characteristics and ecological functionality, which allowed them to subdivide the Madre de Dios Basin to perform the analysis. Despite the large areas under protection Thieme et al. (2007) found several freshwater areas unrepresented in the protected areas scenario, namely five of eight classes of streams, one sub-basin and one of six floodplains. These authors also state that the idea to create protected areas based on terrestrial ecosystems and organisms is inadequate for freshwater ecosystems and species.

The knowledge about the Amazon fishes still presents large gaps and most information is concentrated on commercially important species, while the small-sized fish, which contains the largest portion of the ichthyofaunal diversity are still poorly known (BARLETTA et al., 2010). Even when aquatic ecosystems are discussed in systematic conservation planning, the examples and reasons are taken from migratory and commercial fish species (see Thieme et al, 2007). However, for freshwater ecosystems small fish species are in the group of the most threatened due to habitat loss (Olden et al., 2007; Nogueira et al., 2010). Amazon *terra-firme* forest streams are very rich ecosystems. The composition of the fish fauna of these streams in Central Amazon varies greatly among nearby streams, with high species turnover along the stream continuum (1st, 2nd, 3rd orders) and low abundance per species (MENDONÇA; MAGNUSSON; ZUANON, 2005). A high turnover among habitats were also found by Albert and collaborators (2011) in Ucayali, Yurua and Purus river basins in Peru. These authors compared the fish richness among rivers, lakes and streams and the highest overall richness was found in streams. They also found similar richness among basins but with different taxonomic compositions, and about 64% of the species were restricted to a single basin. Freshwater organisms are limited by the landscape surroundings that subject them to biogeographical constraints and habitat isolation (OLDEN et al., 2010).

There are no basin-wide data about riparian zones of small streams, thought to be the major freshwater ecosystem in the Amazon basin (CASTELLO et al., 2013). The hierarchically nested characteristics of freshwater ecosystems could lead a local impact to propagate along the catchment area, making this ecosystems especially vulnerable to environmental disturbances (CASTELLO et al., 2013; DUDGEON et al., 2006; FAUSH et al., 2002). The vulnerability of freshwater ecosystems and its fishes to anthropogenic impact has been discussed for more than a decade (ABELL, 2002; CASTELLO et al., 2013; DUDGEON et al., 2006; OLDEN et al., 2010), but still little attention has been given to these ecosystems and species in conservation planning (ABELL; ALLAN; LEHNER, 2007; AMIS et al., 2009; BEGER et al., 2010). The increasing number of protected areas in the Amazon stems from the ARPA program, had the main purposes control the deforestation and to meet the demands of traditional populations and sustainable forest production (VERÍSSIMO et al., 2011a). The Brazilian government strategy was due to three reasons:

“First, the need to order the territory and combat illegal deforestation associated with land grabbing. Second, the urgency to protect areas with high biological values. Third, the need to meet the demands of traditional populations and sustainable forest production” (Veríssimo et al., 2011b, p.24)

Thus, the majority of the protected areas in the Brazilian Amazon were created in areas subjected to high anthropogenic pressures (VERÍSSIMO et al., 2011a). Deforestation rates in the Brazilian Amazon only started to decrease in 2005, when there was a similar decrease of deforestation inside IPAs and ITs (NEPSTAD et al., 2006; VERÍSSIMO et al., 2011a). We agreed that in the early 2000’s such strategies were necessary to control the Amazon deforestation, since habitat loss is the highest threat for the regional biota, including stream fishes (DUDGEON et al., 2006; OLDEN; HOGAN; ZANDEN, 2007) and

deforestation is one of its main causes (BARLETTA et al., 2010). Amazon streams depend on allochthonous sources of energy and nutrients, namely the organic matter input from riparian forests. Nevertheless, conservation units selected in the way mentioned above proved to be inefficient for conservation of the Amazon stream species when analyzed in a large, biome-wide scale. Otherwise, the category of conservation Units intended for sustainable use have been questioned, (BARLETTA et al., 2010), since higher deforestation rates were observed in some of these areas (VERÍSSIMO et al., 2011a).

Freshwater ecosystems and species may be less “*sexy*” (as stated by Abell, 2002) than terrestrial and marine ones, but protecting these ecosystems is very important and urgent (ABELL, 2002). The vulnerability and potential threat for Amazon freshwater ecosystems were pointed out by Castello and collaborators (2013), and the conservation of these ecosystems requires an integrated effort involving the scientific community, public and private agencies, and local and regional communities. We agreed with these authors and also believe that the first step to accomplish this goal is adding freshwater species and ecosystems in Systematic Conservation Planning as soon as possible.

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Supplementary S1

Table 1: Area Under Curve and True Skill Statistics values for all species. N- number of occurrence points.

Order	Species	N	AUC	TSS
Characiformes	<i>Hoplias malabaricus</i>	347	0.783	0.007
	<i>Gymnocorymbus thayeri</i>	13	0.795	0.002
	<i>Hemigrammus schmardae</i>	13	0.818	0.004
	<i>Hoplerethrinus unitaeniatus</i>	125	0.821	0.003
	<i>Melanocharacidium pectorale</i>	13	0.834	0.004
	<i>Moenkhausia chrysargyrea</i>	6	0.838	0.001
	<i>Moenkhausia oligolepis</i>	315	0.839	0.008
	<i>Serrasalmus rhombeus</i>	103	0.843	0.003
	<i>Axelrodia lindeae</i>	14	0.852	0.005
	<i>Pyrrhulina zigzag</i>	12	0.856	0.000
	<i>Erythrinus erythrinus</i>	193	0.856	0.008
	<i>Prochilodus nigricans</i>	132	0.858	0.006
	<i>Poptella compressa</i>	78	0.861	0.003
	<i>Hemiodus thayeria</i>	12	0.861	0.001
	<i>Bryconops giacopinii</i>	44	0.864	0.004
	<i>Melanocharacidium dispilomma</i>	38	0.869	0.001
	<i>Jupiaba asymmetrica</i>	6	0.872	0.002
	<i>Myloplus rubripinnis</i>	10	0.878	0.004
	<i>Hemigrammus ocellifer</i>	145	0.878	0.007
	<i>Acestrorhynchus microlepis</i>	106	0.881	0.004
	<i>Pristella maxillaris</i>	8	0.883	0.007
	<i>Bryconops melanurus</i>	178	0.883	0.008
	<i>Bryconops caudomaculatus</i>	174	0.885	0.007
	<i>Hemigrammus stictus</i>	12	0.886	0.005
	<i>Cyphocharax spilurus</i>	105	0.888	0.004
	<i>Hyphessobrycon copelandi</i>	38	0.888	0.001
	<i>Gasteropelecus sternicla</i>	20	0.891	0.002
	<i>Charax condei</i>	8	0.891	0.002
	<i>Carnegiella strigata</i>	79	0.892	0.004
	<i>Nannostomus trifasciatus</i>	58	0.893	0.003
	<i>Moenkhausia cotinho</i>	75	0.895	0.002
	<i>Moenkhausia hemigrammoides</i>	11	0.897	0.004
	<i>Hemigrammus vorderwinkleri</i>	37	0.897	0.002
	<i>Bryconops affinis</i>	54	0.898	0.002
	<i>Hoplias curupira</i>	20	0.901	0.001
	<i>Ammocryptocharax elegans</i>	44	0.902	0.001
	<i>Microschemobrycon geisleri</i>	14	0.903	0.006
	<i>Hemigrammus levis</i>	48	0.908	0.002
	<i>Acestrorhynchus falcatus</i>	24	0.909	0.001
	<i>Hemigrammus microstomus</i>	14	0.909	0.005

<i>Copella nigrofasciata</i>	67	0.911	0.004
<i>Nannostomus marginatus</i>	67	0.911	0.001
<i>Iguanodectes spilurus</i>	51	0.913	0.003
<i>Hemigrammus iota</i>	8	0.913	0.007
<i>Microcharacidium gnomus</i>	6	0.913	0.003
<i>Moenkhausia comma</i>	48	0.914	0.003
<i>Hyphessobrycon bentosi</i>	36	0.915	0.002
<i>Heterocharax virgulatus</i>	18	0.916	0.001
<i>Jupiaba zonata</i>	24	0.917	0.002
<i>Gnathocharax steindachneri</i>	30	0.917	0.003
<i>Elachocharax pulcher</i>	48	0.923	0.000
<i>Hemigrammus melanochrous</i>	20	0.925	0.002
<i>Axelrodia stigmatias</i>	17	0.925	0.001
<i>Iguanodectes geisleri</i>	32	0.928	0.002
<i>Hyphessobrycon heterorhabdus</i>	100	0.928	0.025
<i>Microcharacidium weitzmani</i>	56	0.930	0.003
<i>Carnegiella marthae</i>	24	0.931	0.002
<i>Moenkhausia pirauba</i>	21	0.932	0.002
<i>Charax leticiae</i>	24	0.932	0.002
<i>Leptocharacidium omospilus</i>	5	0.933	0.003
<i>Amazonspinther dalmata</i>	10	0.934	0.010
<i>Crenuchus spilurus</i>	99	0.935	0.008
<i>Jupiaba polylepis</i>	99	0.936	0.005
<i>Odontocharacidium aphanes</i>	23	0.937	0.002
<i>Nannostomus eques</i>	73	0.937	0.005
<i>Jupiaba anteroides</i>	18	0.941	0.009
<i>Iguanodectes variatus</i>	20	0.941	0.002
<i>Paracheiroduon innesi</i>	6	0.941	0.006
<i>Jupiaba poranga</i>	18	0.941	0.014
<i>Bario steindachneri</i>	8	0.942	0.004
<i>Moenkhausia collettii</i>	32	0.942	0.003
<i>Tyttocharax madeirae</i>	25	0.944	0.002
<i>Poptella brevispina</i>	29	0.945	0.001
<i>Nannostomus beckfordi</i>	40	0.945	0.000
<i>Nannostomus digrammus</i>	30	0.945	0.002
<i>Hemigrammus rodwayi</i>	89	0.945	0.005
<i>Copella nattereri</i>	76	0.946	0.010
<i>Jupiaba apenima</i>	23	0.946	0.002
<i>Hemigrammus bellottii</i>	42	0.946	0.005
<i>Hemigrammus analis</i>	33	0.947	0.002
<i>Curimatopsis macrolepis</i>	18	0.949	0.001
<i>Elachocharax junki</i>	22	0.950	0.001
<i>Ammocryptocharax minutus</i>	10	0.951	0.008
<i>Paracheiroduon simulans</i>	6	0.952	0.007
<i>Hemigrammus coeruleus</i>	18	0.954	0.003

	<i>Bryconella pallidifrons</i>	17	0.954	0.002
	<i>Pyrrhulina laeta</i>	19	0.956	0.001
	<i>Microcharacidium eleotrioides</i>	36	0.956	0.005
	<i>Iguanodectes gracilis</i>	6	0.958	0.003
	<i>Bryconops inpai</i>	24	0.960	0.013
	<i>Cyphocharax gouldingi</i>	13	0.960	0.009
	<i>Copella arnoldi</i>	24	0.961	0.004
	<i>Knodus savannensis</i>	19	0.966	0.002
	<i>Copella eigenmanni</i>	9	0.966	0.006
	<i>Moenkhausia diktyota</i>	6	0.967	0.007
	<i>Tytocharax cochui</i>	5	0.972	0.007
	<i>Leporinus klausewitzi</i>	15	0.973	0.016
	<i>Phenacogaster retropinnus</i>	40	0.976	0.011
	<i>Creagrutus ignotus</i>	23	0.977	0.005
	<i>Poecilocharax weitzmani</i>	14	0.979	0.003
	<i>Hemigrammus rhodostomus</i>	9	0.979	0.013
	<i>Elachocharax mitopterus</i>	19	0.981	0.003
	<i>Hemigrammus guyanensis</i>	23	0.982	0.005
	<i>Hyphessobrycon melazonatus</i>	35	0.983	0.006
	<i>Boulengerella lateristriga</i>	14	0.983	0.028
	<i>Priocharax ariel</i>	5	0.984	0.016
	<i>Iguanodectes rachovii</i>	24	0.985	0.004
	<i>Moenkhausia phaeonota</i>	64	0.985	0.013
	<i>Steindachnerina amazonica</i>	5	0.989	0.017
	<i>Hyphessobrycon amapaensis</i>	17	0.990	0.005
	<i>Moenkhausia agnesae</i>	7	0.995	0.054
Siluriformes	<i>Acestridium martini</i>	5	0.971	0.003
	<i>Hisonotus luteofrenatus</i>	5	0.986	0.018
	<i>Tetranematichthys wallacei</i>	5	0.951	0.006
	<i>Acestridium gymnogaster</i>	6	0.865	0.003
	<i>Centromochlus meridionalis</i>	6	0.977	0.036
	<i>Microglanis poecilus</i>	6	0.849	0.002
	<i>Auchenipterichthys punctatus</i>	7	0.931	0.002
	<i>Cetopsis sandrae</i>	8	0.949	0.004
	<i>Farlowella platorynchus</i>	8	0.895	0.007
	<i>Otocinclus caxarari</i>	8	0.872	0.004
	<i>Oxyropsis wrightiana</i>	8	0.997	0.153
	<i>Pariolius armillatus</i>	8	0.977	0.023
	<i>Tatia brunnea</i>	8	0.893	0.003
	<i>Nemuroglanis lanceolatus</i>	9	0.933	0.006
	<i>Stauroglanis gouldingi</i>	10	0.958	0.008
	<i>Hisonotus chromodontus</i>	11	0.985	0.040
	<i>Parotocinclus longirostris</i>	12	0.888	0.011
	<i>Tatia gyrina</i>	12	0.933	0.007
	<i>Brachyglanis microphthalmus</i>	13	0.794	0.012

	<i>Rhamdia muelleri</i>	13	0.938	0.006
	<i>Trachelyopterichthys taeniatus</i>	13	0.893	0.018
	<i>Corydoras elegans</i>	14	0.914	0.005
	<i>Physopyxis lyra</i>	14	0.890	0.007
	<i>Otocinclus mura</i>	15	0.908	0.006
	<i>Nemuroglanis pauciradiatus</i>	16	0.962	0.015
	<i>Corydoras julii</i>	17	0.981	0.002
	<i>Farlowella smithi</i>	18	0.913	0.001
	<i>Physopyxis ananas</i>	18	0.959	0.002
	<i>Trachelyopterus galeatus</i>	18	0.931	0.002
	<i>Scoloplax distolothrix</i>	19	0.914	0.000
	<i>Myoglanis koepckeii</i>	20	0.951	0.002
	<i>Acestridium discus</i>	21	0.980	0.002
	<i>Bunocephalus verrucosus</i>	21	0.956	0.002
	<i>Gladioglanis conquistador</i>	21	0.931	0.003
	<i>Batrochoglanis raninus</i>	26	0.894	0.001
	<i>Tatia intermedia</i>	27	0.871	0.001
	<i>Denticetopsis seducta</i>	29	0.858	0.000
	<i>Imparfinis pristos</i>	29	0.852	0.001
	<i>Imparfinis stictonotus</i>	29	0.925	0.001
	<i>Acanthodoras cataphractus</i>	30	0.894	0.001
	<i>Otocinclus hoppei</i>	31	0.943	0.002
	<i>Megalechis picta</i>	34	0.894	0.000
	<i>Otocinclus vitatus</i>	36	0.886	0.001
	<i>Trichomycterus hasemani</i>	40	0.950	0.002
	<i>Bunocephalus coracoideus</i>	53	0.883	0.001
	<i>Mastiglanis asopos</i>	62	0.881	0.002
	<i>Pimelodella cristata</i>	67	0.883	0.005
	<i>Callichthys callichthys</i>	68	0.795	0.001
	<i>Ituglanis amazonicus</i>	82	0.896	0.004
	<i>Rineloricaria lanceolata</i>	105	0.852	0.002
	<i>Helogenes marmoratus</i>	173	0.904	0.009
Ciprinodontiformes	<i>Rivulus dibaphus</i>	14	0.986	0.029
	<i>Rivulus kirovskiyi</i>	23	0.959	0.007
	<i>Rivulus micropus</i>	63	0.940	0.007
	<i>Rivulus ornatus</i>	21	0.971	0.002
Gymnotiformes	<i>Sternopygus castroi</i>	6	0.934	0.003
	<i>Hypopygus neblinae</i>	8	0.935	0.009
	<i>Gymnotus coatesi</i>	12	0.886	0.007
	<i>Electroforus electrus</i>	16	0.846	0.005
	<i>Gymnotus pendanopterus</i>	16	0.955	0.016
	<i>Rhamphichthys marmoratus</i>	27	0.915	0.003
	<i>Brachyhypopomus beebei</i>	38	0.892	0.001
	<i>Steatogenys duidae</i>	42	0.930	0.001
	<i>Brachyhypopomus bevirostris</i>	45	0.919	0.003

	<i>Gymnotus carapo</i>	71	0.795	0.001
	<i>Gymnorhamphichthys petiti</i>	108	0.904	0.009
	<i>Gymnotus coropinae</i>	121	0.911	0.008
	<i>Sternopygus macrurus</i>	128	0.869	0.003
	<i>Hypopygus lepturus</i>	134	0.884	0.007
Perciformes	<i>Acaronia nassa</i>	94	0.929	0.004
	<i>Aequidens epae</i>	25	0.959	0.001
	<i>Aequidens pallidus</i>	90	0.953	0.021
	<i>Aequidens tetramerus</i>	226	0.871	0.009
	<i>Apistogramma agassizii</i>	85	0.947	0.005
	<i>Apistogramma caetei</i>	34	0.987	0.012
	<i>Apistogramma mendezi</i>	7	0.979	0.011
	<i>Apistogramma pertensis</i>	29	0.980	0.002
	<i>Apistogramma regani</i>	11	0.985	0.014
	<i>Apistogramma rupununi</i>	5	0.996	0.119
	<i>Apistogramma steindachneri</i>	18	0.950	0.001
	<i>Apistogramma taeniata</i>	18	0.976	0.125
	<i>Crenicara punctulatum</i>	17	0.836	0.005
	<i>Crenicichla inpa</i>	70	0.884	0.003
	<i>Crenicichla notophthalmus</i>	16	0.983	0.015
	<i>Crenicichla regani</i>	62	0.890	0.002
	<i>Crenicichla strigata</i>	24	0.931	0.002
	<i>Microphilypnus ternetzi</i>	21	0.931	0.003
	<i>Monocirrhus polyacanthus</i>	45	0.886	0.002
Symbranchiformes	<i>Synbranchus lampreia</i>	11	0.993	0.041
	<i>Synbranchus madeirae</i>	71	0.845	0.002

Considerações finais

Devido à falta de informação em ampla escala sobre as características limnológicas de igarapés na bacia Amazônica, o capítulo 01 desta Tese testou a relação entre as variáveis limnológicas locais e de macroescala. Condições limnológicas locais e variáveis de macroescala foram fortemente correlacionadas na Amazônia brasileira, o que se deve às condições geomorfológicas e o histórico de formação da bacia Amazônica. Portanto, as variáveis de macroescala podem ser usadas para inferir informações sobre variáveis locais, permitindo a modelagem de nicho de espécies de peixes em igarapés da Amazônia brasileira, o que é especialmente importante quando se consideram as enormes lacunas de informação em escala local para esses pequenos corpos d'água.

A partir desses resultados, variáveis de macroescala foram utilizadas como medida do nicho Grinneliano para espécies de peixes de igarapés da Amazônia Brasileira. No capítulo 02 desta Tese foi testada a hipótese de conservação filogenética de nicho em algumas espécies selecionadas de peixes de igarapés. Os resultados mostraram a existência de estrutura filogenética no nicho Grinneliano entre as ordens Characiformes, Siluriformes e Gymnotiformes, mas nenhum padrão filogenético significativo dentro de cada uma das ordens, ao menos para as espécies estudadas. Esses resultados sugerem que a conservação de nicho em nível de ordens, pode limitar a capacidade das espécies de se adaptarem às mudanças climáticas globais em curso e às novas condições do nicho, como observado por Wiens e colaboradores (2010).

Frente às ameaças aos ecossistemas aquáticos e às características de conservação de nicho de algumas espécies de igarapés, foi investigado se as espécies de peixes de igarapés estão sendo conservadas pelas grandes Unidades de Conservação da Amazônia legal Brasileira. Assim, os resultados do capítulo 03 indicaram que as Megareservas na Amazônia não estão protegendo adequadamente (ou integralmente) a ictiofauna de igarapés de terra firme. Essas UCs foram idealizadas e implementadas para proteger organismos e ecossistemas terrestres, com o objetivo de serem grandes o suficiente para cobrir o maior número de fitofisionomias possível. Entretanto, essa maneira de realizar o planejamento sistemático da conservação não tem sido efetiva para a conservação de peixes de igarapés Amazônicos. Assim, para que haja a conservação dos ecossistemas e espécies de peixes de água doce, faz-se necessário a integração entre organismos aquáticos e terrestres no estabelecimento de estratégias para uma conservação biológica efetiva e abrangente na Amazônia brasileira.

Explorado o nicho Grinneliano das espécies de peixes de igarapés da Amazônia é possível obter informações que podem ser utilizadas para conservá-las. Os resultados nos mostraram que o nicho Grinneliano dos peixes de igarapés de terra firme amazônicos possui características que representam bem seu nicho ecológico, podendo ser usados na construção de modelos para suprir a lacuna de informação sobre a distribuição de espécies. Além disso, a característica do nicho ser conservado entre as ordens gera informações sobre uma maior vulnerabilidade desses organismos, em relação aos impactos antrópicos. Esse trabalho mostra claramente que espécies tão pouco conhecidas, e ao mesmo tempo altamente vulneráveis, precisam ser integradas nos planejamentos sistemáticos para conservação da Amazônia.

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