INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Uma questão de escala: Fatores históricos e ambientais estruturam assembleias de anuros do Alto Rio Madeira, Amazônia

RANDOLPHO GONÇALVES DIAS TERCEIRO

Manaus - AM
Junho, 2014

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Uma questão de escala: Fatores históricos e ambientais estruturam assembleias de anuros do Alto Rio Madeira, Amazônia

RANDOLPHO GONÇALVES DIAS TERCEIRO

ORIENTADOR: Dr. IGOR LUIS KAEFER
CO-ORIENTADORA: Dra. ALBERTINA PIMENTEL LIMA

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para a obtenção do título de Mestre em Biologia (Ecologia).

Manaus - AM
Junho, 2014

T315 Terceiro, Randolpho Gonçalves Dias
Uma questão de escala: Fatores históricos e ambientais estruturam assembleias de anuros do Alto Rio Madeira, Amazônia / Randolpho Gonçalves Dias Terceiro. --- Manaus: [s. n.], 2014.
ix, 61 f. : il. color.

Dissertação (Mestrado) --- INPA, Manaus, 2014.
Orientador : Igor Kaefer.
Coorientador : Albertina Pimentel Lima.
Área de concentração : Ecologia

1. Anfíbios. 2. Anuros. 3. Barreira de dispersão. I. Título.

CDD 597.8

Sinopse:

Foi analisada a composição das assembleias de anuros diurnos de liteira em relação à margem do Rio Madeira e variáveis ambientais. Foram utilizadas 98 amostras padronizadas. Pôde ser observado o efeito do Rio Madeira e variáveis ambientais nas diferenças da composição de espécies assembleias de anuros avaliadas. Nós evidenciamos que ambos os elementos históricos e ambientais moldaram a ocorrência e distribuição das espécies de anuros na área de estudo.

Palavras-Chave: Barreira de dispersão; anfíbios; gradiente ambiental; composição de espécies.

DEDICATÓRIA

Dedico esta dissertação ao meu filho Daniel Marques Dias, à minha esposa Gabriela Marques Peixoto Dias, aos meus pais Randolpho Gonçalves Dias Neto e Heleneide Mangueira Carneiro, à minha madrasta Ana Maria Pereira dos Santos Goncalves Dias e aos meus irmãos Emilson Ribeiro Neto, Ana Paula Santos Gonçalves Dias e Bruno Santos Gonçalves Dias.

AGRADECIMENTOS

A Deus, por me dar saúde e força para enfrentar as dificuldades da vida acadêmica.

Ao Dr. Igor L. Kaefer pela orientação deste projeto, além da ajuda na escrita e motivação para a conclusão deste trabalho.

À Dr.ª Albertina P. Lima, pela co-orientação, disposição e pela oportunidade de trabalhar com anuros no momento em que mais precisei.

Aos alunos de pós-graduação Eveline Salvático e Layon Oreste por influenciarem em momentos decisivos na minha carreira acadêmica.

Às pessoas do laboratório que ajudaram com as coletas dos dados para que eu pudesse escrever esta dissertação, Rafael de Fraga, Pedro Ivo Simões e Maria Carmozina de Araújo.

Ào pessoal da herpetologia que contribuiu com seus conhecimentos, fornecendo artigos e palpitando na escrita desta dissertação, Diana Rojas Ahumada, Rafael Filgueira Jorge e Miquéias Ferrão.

Ao MSc. David V. Dias pela ajuda a manusear o programa R, sugerindo as análises de ordenação e o teste de MANOVA.

Ao Dr. Carlos Alberto N. Quesada na ajuda dos cálculos das Somas de Bases (nutrientes do Solo).

A todos os colegas da pós-graduação que me incentivaram a continuar na “batalha” do dia-a-dia acadêmico.

À minha família, pela força e amparo nas horas mais cruciais.

Ao Programa de Conservação de Fauna da Hidrelétrica Santo Antônio Energia, ao qual os dados foram coletados.

À CAPES pela ajuda financeira.

À Coordenação da Pós-graduação em Biologia (Ecologia) do INPA.

“Em algum lugar, pra relaxar, eu vou pedir pros anjos cantarem por mim. Pra quem tem fé, a vida nunca tem fim”.

Anjos (Pra Quem Tem Fé) – O Rappa

RESUMO

História biogeográfica e interações ecológicas atuais têm normalmente sido tratadas de forma separada para explicar padrões em biodiversidade. Nesse estudo, avaliamos de forma integrada os efeitos de fatores biogeográficos e ambientais na estruturação de assembleias de anfíbios anuros diurnos do alto Rio Madeira, sudoeste da Amazônia. Utilizamos um desenho amostral envolvendo 98 unidades padronizadas, distribuídas ao longo de sete localidades cobrindo ambas as margens do curso do rio no estado de Rondônia, Brasil. Procura ativa por anuros foi realizada em três excursões entre fevereiro de 2010 e fevereiro de 2011, com os objetivos de: 1) avaliar o efeito do Rio Madeira como barreira biogeográfica ao nível de assembleia de espécies, e 2) testar a influência de sete variáveis ambientais (estrutura da vegetação, cobertura de vegetação, nutrientes do solo, estrutura do solo, inclinação, altitude e distância da margem do rio) na estrutura espacial das assembleias de anfíbios, separadamente por margem do rio. Doze espécies de anuros diurnos foram registradas, seis das quais foram restritas a uma das margens do rio. Análises de variância multivariada indicaram efeito significativo do rio como barreira. Análises de regressão múltipla sugeriram que as variáveis ambientais que estruturam as assembleias de anuros diferem em cada lado do rio. Encontramos que tanto elementos históricos (em escala regional) como fatores ambientais (em escala local) moldaram a ocorrência e distribuição de espécies de anuros na área de estudo.

Palavras chave: Barreira de dispersão; anuros diurnos; gradiente ambiental; composição de espécies.

ABSTRACT

Biogeographical history and current ecological interactions have usually been addressed separately to explain patterns of biodiversity. In this study, we evaluated the integrated effects of biogeographical and environmental factors in structuring the diurnal amphibian anuran assemblages of the upper Madeira River, southwestern Amazonia. We used a sampling design involving 98 standardized units, distributed across seven locations covering both banks of the river's course in the state of Rondônia, Brazil. An active search for frogs was performed in three trips between February 2010 and February 2011, with the objectives of: 1) to evaluate the effect of the Madeira River as a biogeographic barrier at the species assemblage level, and 2) test the influence of seven environmental variables (vegetation structure, vegetation cover, soil nutrients, soil structure, slope, altitude and distance from the river bank) on the spatial structure of the frog assemblages, separately by river bank. Twelve species of diurnal frogs were recorded, six of which were restricted to one of the river margins. Multivariate analysis of variance indicated a significant effect of the river as a barrier. Multiple regression analyzes suggested that the environmental variables structuring frog assemblages differ on either side of the river. We found that both historical elements (on a regional scale) and environmental actors (at a local scale) shaped the occurrence and distribution of frog species in the study area.

Key words: Dispersal barrier; frogs; environmental gradient; species composition

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

INTRODUÇÃO GERAL

A ecologia de comunidades tem como uma de suas principais abordagens a busca pelo conhecimento de padrões de distribuição, abundância e interações das espécies na natureza, procurando entender como estas espécies se organizam no tempo e espaço em função de variáveis ambientais (Ricklefs & Schluter, 1993; Brown, 1995). Por exemplo, características edáficas e topográficas influenciam a distribuição de espécies de plantas de sub-bosque e de árvores (Lescure & Boulet, 1985; Kahn & Castro, 1985; Clark *et al*., 1999; Kinupp & Magnusson, 2005), e a variabilidade do microhábitat ou composição do solo podem influenciar na variação da composição de espécies de formigas (Vasconcelos *et al.*, 2003) e aves (Bueno *et al.*, 2012) .

No caso de anfíbios anuros, estudos que abordaram a influência do ambiente na estruturação das assembleias indicaram diferentes fatores que determinam sua distribuição em macroescala espacial como o relevo, o clima e os grandes tipos vegetacionais (Duellman, 1999; Silva *et al.*, 2012). Diversos estudos têm abordado e discutido a extensão da influência da heterogeneidade do habitat em mesoescala (e.g. Parris, 2004; Ernst & Rödel, 2005; Vasconcelos & Rossa-Feres, 2008; Vasconcelos *et al*., 2009; Keller *et al*., 2009; Silva *et al*., 2011, 2012; Santos *et al*., 2012). No entanto, os resultados obtidos são contrastantes, não permitindo a detecção de padrões gerais relacionados ao tema.

Na Amazônia Central estudos verificaram efeito significativo da altitude (Condrati, 2009; Rojas-Ahumada *et al*., 2012; Ribeiro-Jr *et al*., 2012), densidade de árvores (Menin *et al*., 2007, 2011; Condrati, 2009), distância do igarapé (Condrati, 2009; Menin *et al*., 2011; Rojas-Ahumada *et al*., 2012), composição do solo (Menin *et al*., 2007; Condrati, 2009; Ribeiro-Jr *et al*., 2012), profundidade e volume de serapilheira (Menin *et al*., 2007, 2011; Rojas-Ahumada *et al*., 2012) e topografia (Menin *et al*., 2007, 2011; Ribeiro-Jr *et al*., 2012) na estruturação de comunidades de anuros, e revelaram que essas variáveis não desempenharam o mesmo papel nos diferentes locais estudados. Mesmo assembleias de anuros em áreas de estudo proximamente localizadas, estudadas de acordo com a mesma metodologia, tiveram suas composições quanti e qualitativas correlacionadas com diferentes fatores ambientais (Condrati 2009; Menin *et al*., 2011; Rojas-Ahumada *et al*., 2012), sugerindo que a relação entre o ambiente e a composição das assembleias em mesoescala possui natureza idiossincrática. A maior parte dos estudos sobre anfíbios anuros tem sido conduzida na região norte da Amazônia Central (Rodrigues, 2006; Menin *et al*., 2007;

2011; Condrati, 2009; Rojas-Ahumada *et al*., 2012, Ribeiro-Jr *et al*., 2012). Os poucos estudos realizados na porção sul da Amazônia (e.g., Bernarde et al., 1999; Bernarde, 2007; Bernarde & Kokubum, 2009; Simões, 2010; Tsuji-Nishikido *et al*., 2012), não avaliaram assembléias de anuros em relação à influência de variáveis ambientais.

Alternativamente à ênfase conferida a fatores ambientais na estruturação de assembleias, Hubbell (2001) propôs a Teoria Neutra, segundo a qual processos probabilísticos na colonização e extinção dos indivíduos nos habitats podem explicar as diferenças de composição e abundância relativa das espécies. Para isso, a Teoria Neutra assume que não há nenhuma diferença entre indivíduos em termos de taxa de sobrevivência *per capita* ou em suas respostas às variáveis ambientais (Hu *et al*., 2006; Zhou & Zhang, 2008). Há uma grande discussão da Teoria Neutra na comunidade científica, em que estudos questionam os seus fundamentos, enquanto outros a corroboram com base em evidências empíricas, contribuindo ao debate a respeito de sua validade e generalidade (Cassemiro & Padia, 2008).

Além dos fatores ambientais, fatores históricos e/ou biogeográficos (*e.g.*, grau de isolamento da área, presença de barreiras à dispersão) são relevantes na estruturação das assembleias. Áreas com clima e estrutura da vegetação similar podem apresentar composição de espécies diferentes dependendo de fatores históricos (Pianka, 1973). No entanto, antes de creditarem-se a efeitos históricos os padrões de distribuição das espécies para áreas onde os fatores ambientais analisados não são fatores explicativos, estudos replicáveis e com desenhos amostrais bem estruturados devem ser realizados (Magnusson, 1997).

Alguns estudos avaliaram o efeito histórico de grandes rios amazônicos em nível de população (e.g., *Hemitriccus spp*. - Cohn-Haft, 2000; *Allobates femoralis* - Simões, 2010; *Psophia spp.* - Ribas *et al*., 2011; *Allobates spp*. - Kaefer *et al*., 2013) e comunidade (e.g., primatas - Ayres & Clutton-Brock, 1992; Passeriformes - Hayes & Sewlal, 2004; ; aves - Pomara *et al*., 2013) e detectaram o efeito dos mesmos como barreiras à dispersão de organismos, levando ao isolamento entre populações e comunidades de margens opostas. Em contrapartida, um estudo realizado no Rio Juruá (Sudoeste da Amazônia) demonstrou que a diferença na composição de anuros não pode ser explicada pelo rio como barreira (Gascon *et al*., 2000). Neste caso, a dinâmica da formação dos meandros que compõem o leito do rio deve ter permitido múltiplos eventos de dispersão de indivíduos no decorrer do tempo. Assim, a hipótese de rios como barreiras, a qual teve origem a partir das observações de Alfred R. Wallace (1852), tem recebido amplo suporte, especialmente em relação ao papel de rios amazônicos não-meândricos como fatores geográficos vicariantes ao longo da história (Antonelli et al. 2010).

Sendo assim, este estudo tem como objetivo avaliar o efeito de fatores ecológicos (ambientais) e histórico (biogeográfico) na estruturação espacial de assembleias de anuros diurnos na região do Alto Rio Madeira, sudoeste da Amazônia. Para isso, foi selecionado um sistema de estudo com múltiplas unidades amostrais padronizadas, distribuídas ao longo de ambas as margens do Rio Madeira, o qual é reconhecido como uma importante barreira biogeográfica. Mais especificamente, objetivamos: (I) avaliar o efeito do Rio Madeira como barreira biogeográfica em nível de comunidade; (II) testar em cada margem se os fatores abióticos exercem papel significante na estruturação espacial das assembleias de anuros e se os fatores ambientais são os mesmos para ambas as margens. Esperamos observar efeito do rio como barreira biogeográfica e que diferentes fatores ambientais desempenhem papel significante na composição das assembleias em cada margem do rio.

OBJETIVOS

Avaliar o efeito de fatores ecológicos (ambientais) e histórico (biogeográfico) na estruturação espacial de assembleias de anuros diurnos na região do Alto Rio Madeira, sudoeste da Amazônia. Para isso, foi selecionado um sistema de estudo com múltiplas unidades amostrais padronizadas, distribuídas ao longo de ambas as margens do Rio Madeira, o qual é reconhecido como uma importante barreira biogeográfica. Mais especificamente, objetivamos: (I) avaliar o efeito do Rio Madeira como barreira biogeográfica em nível de comunidade; (II) testar em cada margem se os fatores abióticos exercem papel significante na estruturação espacial das assembleias de anuros e se os fatores ambientais são os mesmos para ambas as margens.

Capítulo I[1]

---

[1] Manuscrito formatado de acordo com as normas da revista Biotropica.

LRH: Dias-Terceiro, Kaefer, Fraga, Araújo, Simões, and Lima

RRH: Spatial structure of anuran assemblages

A Matter of Scale: Historical and Environmental Factors Structure Anuran Assemblages from the Upper Madeira River, Amazonia

Randolpho Gonçalves Dias-Terceiro[2]; Igor Luis Kaefer[2]*; Rafael de Fraga[1]; Maria Carmozina de Araújo[1]; Pedro Ivo Simões[1]; Albertina Pimentel Lima[1]

[1]Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, CEP 69011-970, Manaus, Amazonas, Brazil

[2]Instituto de Ciências Biológicas, Universidade Federal do Amazonas, CEP 69077-000, Manaus, Amazonas, Brazil.

Received __________; revision accepted __________ .

---

* Corresponding Author; e-mail: kaefer@ufam.edu.br

Abstract

Biogeographical history and current ecological interactions have usually been addressed separately to explain patterns of biodiversity spatial distribution. In this study, we evaluated the integrated effects of biogeographical and environmental factors in structuring the diurnal amphibian anuran assemblages of the upper Madeira River, southwestern Amazonia. We used a sampling design involving 98 standardized units, distributed across seven locations covering both banks of the river's course in the state of Rondônia, Brazil. Active search for frogs was performed in three campaigns between February 2010 and February 2011, aiming to: 1) evaluate the effect of the Madeira River as a biogeographic barrier at the species assemblage level, and 2) test the influence of seven environmental variables (vegetation structure, vegetation cover, soil nutrients, soil structure, slope, altitude and distance from the river bank) on the spatial structure of the frog assemblages, separately on each riverbank. Thirteen species of diurnal frogs were recorded, six of which were restricted to one of the river margins. Multivariate analysis of variance indicated a significant effect of the river as a barrier. Multiple regression analyses suggested that the environmental variables structuring frog assemblages differ on either side of the river. We found that both historical elements (on a regional scale) and environmental actors (at a local scale) shaped the occurrence and distribution of frog species in the study area.

Key words: Amphibia; Anura; diurnal frogs; environmental gradients; riverine barrier; Rondônia; species composition.

Resumo

A história biogeográfica e as interações ecológicas atuais têm sido normalmente tratadas de forma separada para explicar padrões de distribuição espacial da biodiversidade. Nesse estudo, avaliamos de forma integrada os efeitos de fatores biogeográficos e ambientais na estruturação de assembleias de anfíbios anuros diurnos do alto Rio Madeira, sudoeste da Amazônia. Utilizamos um desenho amostral envolvendo 98 unidades padronizadas, distribuídas ao longo de sete localidades cobrindo ambas as margens do curso do rio no estado de Rondônia, Brasil. Procura ativa por anuros foi realizada em três excursões entre fevereiro de 2010 e fevereiro de 2011, com os objetivos de: 1) avaliar o efeito do Rio Madeira como barreira biogeográfica ao nível de assembleia de espécies, e 2) testar a influência de sete variáveis ambientais (estrutura da vegetação, cobertura de vegetação, nutrientes do solo, estrutura do solo, inclinação, altitude e distância da margem do rio) na estrutura espacial das assembleias de anfíbios, separadamente por margem do rio. Treze espécies de anuros diurnos foram registradas, seis das quais foram restritas a uma das margens do rio. Análises de variância multivariada indicaram efeito significativo do rio como barreira. Análises de regressão múltipla sugeriram que as variáveis ambientais que estruturam as assembleias de anuros diferem em cada lado do rio. Encontramos que tanto elementos históricos (em escala regional) como fatores ambientais (em escala local) moldaram a ocorrência e distribuição de espécies de anuros na área de estudo.

DEPENDING ON THE SPATIAL SCALE OF THE ANALYSIS DIFFERENT PROCESSES CAN AFFECT THE taxonomic composition and functional structure of species assemblages (Vellend 2010, Montaña *et al*. 2014). Patterns of community structure derive from interactions between regional historical (*e.g.*, Ricklefs & Renner 2012) and local ecological processes (Cornell & Lawton 1992, Ricklefs 2004, Algar *et al*. 2011). At the regional scale, historical biogeographic factors (*e.g.*, degree of isolation of the area, the presence of barriers to dispersal) are the main determinants of biodiversity (Jackson *et al*., 2001, Algar *et al*. 2011). At the local scale, the assemblages that make up a particular community should be strongly influenced by both abiotic environmental factors and by interactions between species (Huston 1999, Brooker *et al*., 2009, Mouchet *et al*. 2013). Abiotic factors are often considered to act as environmental filters that, due to the limiting environmental conditions they impose, determine which species will occur at a given site (Keddy 1992).

River barriers are one of several historical factors that can affect the structure of species assemblages on a regional scale. Originally proposed by Alfred R. Wallace (1852), the riverine barrier hypothesis has received wide support, especially for the role of non-meandering rivers as geographical vicariant factors in Amazonian history (Antonelli *et al.* 2010). Several studies have evaluated the historical effect of large Amazonian rivers and shown they function as barriers to dispersal of organisms, leading to the isolation of populations and communities on opposite river banks, and the delimitation of areas of endemism within the biome (Cohn-Haft 2000, Ron 2000, Hayes & Sewlal 2004, Ribas *et al.* 2011; Kaefer *et al.* 2013, Pomara *et al.* 2013).

At the regional scale, areas with similar environmental factors, such as climate and vegetation, may have a different species composition depending on historical factors (Pianka 1973). At the local scale, sampling strategy can have a substantial impact on results of assemblage studies, and an absence of significant results may be partly due to the use of variables sensitive to the uncertainties in the processes of assemblage formation (Aiba *et al.* 2013). Thus, when current environmental factors do not explain observed patterns of species distribution, replicable studies with well-structured sampling designs should be performed before stating that historical effects are the underlying cause (Magnusson 1997).

Studies at the local scale have evaluated the effect of environmental factors on species composition in tropical assemblages. For example, soil and topographical characteristics can influence the distribution of plant species and understory trees (Kahn & Castro 1985, Lescure & Boulet 1985, Clark *et al.* 1999, Kinupp & Magnusson 2005), while the variability of microhabitats and soil constitution may influence variation in the species composition of ant (Vasconcelos *et al*. 2003), snake (Fraga *et al.* 2011), and bird assemblages (Bueno *et al.* 2012). For structuring anuran communities in Central Amazonia, studies have found significant effects for altitude (Condrati 2009, Ribeiro-Jr. *et al*. 2012, Rojas-Ahumada *et al*. 2012), tree density (Menin *et al*. 2007, 2011; Condrati 2009), distance to streams (Condrati 2009, Menin *et al*. 2011, Rojas-Ahumada *et al.* 2012), soil texture (Menin *et al*. 2007, Condrati 2009), depth and volume of leaflitter (Menin *et al*. 2007, 2011; Rojas-Ahumada *et al*. 2012) and topography (Menin *et al.* 2007, 2011), although they have also revealed that these variables did not play the same role at all sites.

Even assemblages of frogs inhabiting geographically close study areas and sampled according to identical protocols have been found to have their quantitative and qualitative compositions correlated with different environmental factors (Condrati 2009, Menin *et al.* 2011, Rojas-Ahumada *et al.* 2012). These suggest that, at the local scale, the relationships between the environment and amphibian assemblage composition have an idiosyncratic nature. Most studies of amphibians have been conducted in the northern part of central Amazonia (Menin *et al*. 2007, 2011; Condrati 2009; Ribeiro-Jr. *et al.* 2012; Rojas-Ahumada *et al.* 2012). The few studies conducted south of the Amazon River (*e.g.*, Bernarde *et al.* 1999, Bernarde 2007) have not focused on the influence of environmental variables on anuran assemblage composition.

Consequently, this study aimed to evaluate the effect of ecological (environmental) and historical (biogeographic) factors on the spatial structure of assemblages of diurnal frogs along the upper Madeira River, southwestern Amazonia, which is widely recognized as an important biogeographical barrier. For this, a study system that used multiple standardized sampling units distributed along both banks of the Madeira River was deployed. Overall, we aimed to investigate the effect of regional and local factors in the same study system. More specifically, we aimed to: (1) evaluate the effect of the Madeira River as biogeographical barrier at the community level; and (2) test, on each bank, which abiotic factors play a significant role in the spatial structure of frog assemblages. We predicted the river would act as a biogeographical barrier at the mesoscale, and that, at the microscale, different environmental factors would play a significant role in the composition of the assemblages on each side of the river. Knowledge on species composition and distribution along the Madeira River banks is particularly relevant in view of the drastic human-driven environmental changes to which the area has been subject (Fearnside 2014).

METHODS

STUDY AREA.—The sampled area is located on the upper Madeira River, upstream of the city of Porto Velho, in the northern region of the state of Rondônia (Fig.1). The Madeira River is the main southern tributary of the Amazon River. Its basin covers an area of almost 1.4 million km2, 23 percent of the Amazon Basin coverage (Muniz et al. 2013). While the landscape on the right bank of the Madeira River is formed by an extension of the Western Amazonian plateau

(Pliopleistocene sediments), the relief of the left bank consists of tabular formations of this same plateau and dissected fragments of the Southern Amazonian Plateau, underlain by Precambrian sediments of the Xingu Complex (DNPM 1978).

The region has experienced pronounced human impact over the last 100 years, resulting in substantial changes to the original vegetation cover. The vegetation of the study area is characterized by Open and Dense tropical rainforest types (with large trees). The soil is predominantly red-yellow latosols, but argisols and gleissols can be found (Choi 2012).

The climate is warm and humid, with average annual temperatures ranging between 24 and 26°C. According to rainfall data obtained between 1982 and 2009 by the National Water Agency (ANA), greatest rainfall occurs between October and April, and lowest rainfall between June and September. Average annual rainfall is 1733 mm, with a maximum of 245 mm in March and a minimum of 26 mm in July. The relative average humidity is 77 percent in the dry season and 88 percent in the rainy season (Horbe *et al*. 2013).

SAMPLING DESIGN.—We collected data in seven sampling locations (grids), each comprising of two trails 5 km long, parallel to each other and approximately perpendicular to the river course. Data was obtained with the support of the Wildlife Conservation Program from Santo Antônio Energia, the concessionaire responsible for building and operating the Santo Antônio Hydroelectric Plant located at the upper Madeira River in the city of Porto Velho, Rondônia, Brazil (08^{o}48’04,0" S; 63^{o}56’59,8" W). Six sampling grids were located on the banks of the Madeira River (two on the right bank and four on the left), with an additional grid on the right bank of Jaci-Paraná River, a southern tributary of the Madeira River (Fig. 1).

In each grid, 14 permanent sampling plots were established, distributed evenly along the two 5 km trails. The plots were positioned 500, 1000, 2000, 3000, 4000 and 5000 m from the river margin. The configuration of the grids, distribution and characteristics of sampling plots followed the RAPELD biodiversity sampling protocol (Magnusson *et al.* 2013). This has allowed the results obtained to be compared between different biological groups and sample areas that use this sampling system.

General guidelines detailing the characteristics of sampling plots can be found at http://ppbio.inpa.gov.br. Sampling grids of the right bank were named as Jirau-Direito (JD), Jaci-Paraná (JP) and Morrinhos (MO). On the left bank, the grids were Jirau-Esquerdo (JE), Ilha Pedra (IP), Ilha Bufalo (IB) and Teotônio (TE).

COLLECTION EFFORT.—Three campaigns were conducted: (1) 24 February 2010 to 26 April 2010; (2) 5 to 26 November 2010; and (3) 13 January 2011 to 4 February 2011. During each campaign, all plots were sampled. Within each plot, visual and auditory searches (Campbell & Christman 1982) were conducted over an area 10 m wide by 250 meters long, during which we recorded the number of specimens of each species heard or observed at each 10 m segment, totaling 25 segments per plot. Frequency of encounter per segment (maximum of 25) was used to indicate abundance of individuals per plot. This procedure aimed to minimize multiple counting of a single individual. Sampling at each plot lasted 40 to 60 minutes and occurred at evening twilight (1630 to 1830 h). Species that did not vocalize during daytime, but which were recorded visually, were not considered in the analysis. Maximum number of individuals of each species recorded among the three campaigns was used as a measure of species abundance per plot in all analyses. Species belonging to a single genus with currently undefined taxonomic status were morphotyped sequentially (*e.g.*, *Allobates* sp1, *Allobates* sp2, *Allobates* sp3).

REGIONAL SCALE ANALYSES.—To evaluate the effect of the Madeira River as a biogeographic barrier at the regional level, we used non-metric multidimensional scaling (NMDS), which reduces dimensionality of species composition data to one axis of a multivariate ordination (Faith *et al.* 1987, Austin 2013). Dissimilarities in species composition between plots were estimated by the Jaccard Index, which gives greater importance to rare species in the sample. To test whether there was segregation in the qualitative structure of the frog assemblages between sample units on different sides of the river, we conducted an analysis of variance (ANOVA) where the dependent variable was the NMDS axis, and the factor was the river bank (right or left). Two NMDS axes were related to visualize the segregation of species compositions in the frog assemblages on the two sides of the river.

LOCAL SCALE ANALYSES.—The following environmental variables were measured in each plot: (1) vegetation structure - VS; (2) soil nutrients – SN; (3) soil structure (proportion of clay) – SS; (4) extent of vegetation cover - EVC; (5) altitude – Alt; (6) slope; and (7) distance from the river bank. Details of the methods used to measure the variables are provided in Appendix S1.

To assess the relationship between environmental variables and species composition (NMDS axis) of diurnal leaf litter frogs, we used multiple linear regression models. The ordinations with quantitative data were based on a matrix of similarities calculated with the Bray-Curtis index (Austin 2013). Models comprised five variables that showed no autocorrelation with each other, since correlated variables carry the same information and could potentially mask or enhance patterns in additive multiple linear models (Magnusson & Mourão 2005). Descriptive statistics of environmental data are presented in Table S1.

The sampling sites were included in the regression models to assess the effect of sampling site-specific environmental variables. Thus, our overall multiple regression model was: NMDS= a + b(sites) + b(VS)+b(SN)+b(SS)+b(EVC)+b(Alt). A multiple regression model was created for the left and right banks to assess if the variables that structure diurnal frog assemblages are the same on both sides of the river. Analyses were performed with the metaMDS function, using the Vegan package (Oksanen *et al.* 2010) in R statistical computing environment (R Development Core Team 2009).

RESULTS

A total of 13 species, distributed in four genera and three families, were recorded for the study area (Table S2). Ordination of plots along one NMDS axis captured 50 percent of the variation in species composition. The diurnal frog assemblages differ significantly between banks of the Madeira River (ANOVA: $F_{1,89} = 19.99$, $P <0.01$). The proportional distribution of distances among plots along the two NMDS axes showed dissimilarity in species composition between frog assemblages on each river margin (Fig. 2). This difference is mostly due to the presence of five species restricted to the left and one to the right margin of the river (Fig. 3).

NMDS ordination of species composition in sampling units distributed on the left margin captured 68.33 percent of the data variation. A multiple regression model using the NMDS axes that summarized species composition (dependent variable) and environmental factors (independent variable) explained 52.6 percent of the variation in frog species composition (NMDS = - 0.95 + 0.79site + 1.29SS + 0.02EVC + 0.67Alt + 0.25SN + 1.83VS; F = 5.82; R^2 = 0.526; $P = 0.02$). Sampling site did not affect overall species composition in the left margin ($F_{1,41} = 1.62$; $P = 0.19$). The environmental variables that contributed significantly to the model were altitude ($F_{1,41} = 4.13$, $P = 0.04$), proportion of clay in the soil ($F_{1,41} = 7.89$, $P <0.01$) and vegetation structure ($F_{1,41} = 11.19$, $P < 0.01$). As expected, some species were widely distributed along the entire environmental gradient, while others occupied smaller portions of it. For example, the presence of *Allobates* sp1, *Allobates* sp4, *Adelphobates quinquevittatus* and *Ameerega picta* was more strongly associated with locations with fewer trees, whereas *Allobates* sp2 was generally detected in sites with relatively higher tree densities (Fig. 4).

On the right bank, ordination of species composition by NMDS captured 55.19 percent of the variation in the diurnal frog assemblage. A multiple regression model between the NMDS (dependent variable) axis and environmental factors (independent variable) explained 73.8 percent of the total variance in species composition (NMDS = 0.04 + 4.06site + 0.01SS + 0.08EVC + 0.5Alt + 0.02SN + 0.08VS; $F = 0.41$; $R^2 = 0.738$; $P = 0.52$). There were differences in species composition among sites on the right bank ($F_{2,29} = 18.31$, $P < 0.01$). None of the environmental variables contributed significantly to the model ($P > 0.484$ in all cases). The right bank Jirau and Jaci-Direito grids have species compositions similar to each other, but different to those found at Morrinhos site (Fig. 5). Following this result, we generated a new right bank NMDS ordination using data from Jirau and Jaci-Direito sites, which captured 65.61 percent of the variation in species composition in the assemblages. A multiple regression model between the NMDS axis (dependent variable) and environmental factors (independent variables) explained 16.85 percent of the variance (NMDS = 0.62+ 0.01SS – 0.0008EVC - 0.01Alt – 0.15SN + 0.0003VS; $R^2 = 0.1685$; $F_{5,20} = 0.81$; $P = 0.55$). None of the environmental variables contributed significantly to the model ($P > 0.197$ in all cases).

DISCUSSION

As a regional barrier, we found the Madeira River has a strong effect on frog species assemblage composition: five species occur only on the left margin (*Allobates* sp2, *Allobates* sp4, *Allobates hodli*, *Allobates nidicola*, *Ameerega trivittata*) and one species is restricted to the right margin (*Allobates* sp3). Therefore, the river course currently restricts the geographic distribution of nearly half the species surveyed, thus determining the observed divergence in assemblage composition of diurnal leaf litter frogs on either side of the river. At the regional scale, environmental variables capable of predicting species composition were different on each river bank. Consequently, we have demonstrated that, in a single study system, ecological processes can operate on a variety of spatial scales (*sensu* Levin 1992), creating patterns that can be perceived differently depending on the survey coverage.

In order to understand a biological system, it is important to study it at a scale appropriate to the issues under investigation, and develop models that enable connections between scales to be made (Chave 2013). Patterns of species composition at regional scales (*e.g.*, riverbanks, in this study), are usually defined by the dispersion ability, and hence geographical distribution of the study organisms, whereas at the local scale such patterns are commonly defined by the spatial extent of ecological interactions among and between individual species and the surrounding environmental factors, all of which could be evaluated by means of the sampling design deployed herein (Srivastava 1999, He *et al*. 2005, Mouchet *et al.* 2013). However, it is important to emphasize that categorizing spatial scales is a subjective exercise, heavily dependent on the biological processes that one wants to investigate, and on the focal organism (Sobral & Cianciaruso 2012).

Studies across a range of different taxonomic groups have shown that large Amazonian rivers affect species composition on opposite riverbanks (*e.g.*, plants, Dexter *et al*. 2012; birds, Hayes & Sewlal 2004; Pomara *et al.* 2013; Primates, Ayres & Clutton-Brock 1992). These studies have demonstrated that species composition in most assemblages diverged as would be predicted if rivers were acting as dispersal barriers. In contrast, a single study has used a similar sampling design to evaluate the composition of frog species assemblages on opposite sides of a large Amazonian river in the past, concluding that the Juruá River does not limit amphibian assemblages with distinct species composition on each riverbank (Gascon *et al.* 2000). However, it is well established that the Juruá is extremely meandering, experiencing regular shifts of its course due to sediment deposition dynamics, hence not exerting important dispersal effects on frog assemblages, nor on intraspecific differentiation of some frog taxa (Gascon *et al.* 1996, 1998, 2000; Lougheed *et al.* 1999). Thus, the Juruá should not be considered a model system applicable to other Amazon rivers when questions regarding differences in amphibian species composition are addressed. Indeed, it has been emphasized that the action of rivers as barriers should not be treated as a general rule for the Amazonian biome (Ayres & Clutton-Brock 1992, Colwell 2000, Leite & Rogers 2013), since Amazonian rivers vary greatly in terms of their age, water flow, width, carried sediments and channel dynamics.

This study is pioneer in the investigation of the complex suite of effects that accompany the role of a great Amazonian river in spatially structuring a set of amphibian species. Previous studies have noted that large rivers, including the lower course of the Madeira, are associated with intraspecific differentiation-in genetic markers and phenotypes of some anuran species (*e.g.*, Funk *et al.* 2007; Fouquet *et al.* 2012; Kaefer *et al*. 2012, 2013; Tsuji-Nishikido *et al.* 2012). However, this is not true for all species: it was reported, for example, that at upper and medium sections the Madeira River does not function as a diversifying barrier for the *Allobates femoralis* complex (Simões *et al.* 2008, Simões 2010).

The composition of frogs on the left bank of the Madeira River altered in association with gradients in altitude, vegetation structure and proportion clay content in the soil. However, the same variables did not affect the species composition on the right bank, where study plots (collection sites) exerted a stronger effect on species composition in relation to environmental characteristics. The variables that shaped the composition of diurnal frog assemblages on the left bank have been previously reported as key factors associated with compositional divergence in amphibian species composition in other studies conducted in Amazonia (Menin *et al.* 2007, 2011; Condrati 2009; Ribeiro-Jr. *et al.* 2012; Rojas-Ahumada *et al*. 2012; Cortés-Gómez *et al*. 2013), and Brazilian Atlantic Forest (reviewed by Siqueira *et al*. 2014). On the other hand, this combination of variables was not the same in any other study site. For example, Condrati (2009) and Ribeiro-Jr. *et al.* (2012) both reported an effect of altitude on the composition of frog assemblages. However, the vegetation structure affected only the assemblages studied by Condrati (2009) where the habitats were more heterogeneous.

For frogs, soil structure can affect species abundance (Woinarski *et al*. 1999, Watling 2005), species richness (Woinarski *et al.* 1999) and assemblage composition (Rojas-Ahumada *et al*. 2012). However, the effect of this variable may not be consistent, for there are recorded cases in which the structure of the soil did not exerted such effects (Allmon 1991; Ribeiro-Jr. *et al*. 2012; present study, right bank). It is also important to note that the structure of the soil affects frogs indirectly, as it can have an effect on the occurrence of small invertebrates (Vasconcelos *et al*. 2003), and these, by being part of the diet of frogs (Vitt & Calldwell 1994), should affect frog spatial distribution more directly (Rojas-Ahumada 2010).

Besides illustrating the roles of both historical and environmental characteristics on the structure of a diurnal anuran community at regional and local scales, respectively, this study provides a striking example of the fine-scale heterogeneity of the species-rich Amazonian biota. The pattern observed along the upper Madeira evokes the image of Amazonia as an "archipelago of distinct areas of endemism separated by major rivers" (Silva *et al*. 2005). Together with the high proportion of undescribed, cryptic, species in our sample, this calls attention to the need to characterize alpha, beta and functional anuran diversities within individual interfluves in order to establish conservation priorities along the Madeira River, a region increasingly threatened by deforestation and economic development.

Acknowledgments

We thank Santo Antônio Energia S.A. for providing funding and logistics for our field work. Collection permits were provided to A.P. Lima by RAN-ICMBio/IBAMA (permanent licence nº 13777-2).

Literature cited

AIBA, M., M. KATABUCHI, H. TAKAFUMI, S. S. MATSUZAKI, T. SASAKI, AND T. HIURA. 2013. Robustness of trait distribution metrics for community assembly studies under the uncertainties of assembly processes. Ecology. 94: 2873–2885.

ALGAR, A. C., J. T. KERR, AND D. L. CURRIE. 2011. Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. Ecology. 92: 903–914.

ALLMON, W. D. 1991. A plot study of forest floor litter frogs, Central Amazon, Brazil. J Trop Ecol. 7: 503–522.

ANTONELLI, A., A. QUIJADA-MASCAREÑAS, A. J. CRAWFORD, J. M. BATES, P. M. VELAZCO, AND W. WÜSTER. 2010. Molecular studies and phylogeography of Amazonian tetrapods and their relation to geological and climatic models. In C. Hoorn and F. P. Wesselingh (Eds.), Amazonia, landscape and species evolution, pp. 386–403. Blackwell Publishing, Oxford, UK.

AUSTIN, M. P. 2013. Inconsistencies between theory and methodology: a recurrent problem in ordination studies. J Veg Sci. 24: 251–268.

AYRES, J. M., AND T. H. CLUTTON-BROCK. 1992. River boundaries and species range size in Amazonian primates. Am Nat. 140: 531–537.

BERNARDE, P. S. 2007. Ambientes e temporada de vocalização da anurofauna no Município de Espigão do Oeste, Rondônia, Sudoeste da Amazônia - Brasil (Amphibia: Anura). Biota Neotropica. 7: 87–92.

BERNARDE, P. S., M. N. C. KOKUBUM, R. A. MACHADO AND L. ANJOS. 1999. Uso de habitats naturais e antrópicos pelos anuros em uma localidade no Estado de Rondônia, Brasil (Amphibia: Anura). Acta Amazonica. 29: 555-562.

BROOKER, R. W., R. M. CALLAWAY, L. A. CAVIERES, Z. KIKVIDZE, C. J. LORTIE, R. MICHALET, F. I. PUGNAIRE, A. VALIENT-BANUET, AND T. G. WHITHAM. 2009. Don't diss integration: a comment on Ricklefs's disintegrating communities. Am Nat. 174: 919–921.

BUENO, A. S., R. S. BRUNO, T. P. PIMENTEL, T. M. SANAIOTTI, AND W. E. MAGNUSSON. 2012. The width of riparian habitats for understory birds in an Amazonian forest. Ecol Appl. 22: 722–734.

CAMPBELL, H. W. AND S. P. CHRISTMAN, 1982. Field techniques for herpetofaunal community analysis. In: N. J. Scott (Ed.). Herpetological Communities: a Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologist's League, pp. 193–200. U.S. Dept. of Interior, Fish and Wildlife Service - Wildlife Research Report, Washington, USA.

CAVALCANTE, M. M. A. 2012. Hidrelétricas do Rio Madeira - RO: território, tecnificação e meio ambiente. PhD Dissertation. Universidade Federal do Paraná, Curitiba.

CHAVE, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecol Lett. 16: 4–16.

CLARK, D. B., M. W PALMER, AND D. A. CLARK. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology. 80: 2662–2675.

COHN-HAFT, M. 2000. A case study in amazonian biogeography: Vocal and DNA sequence variation in *Hemitriccus flycatchers*. PhD Dissertation. Luisiana State University.

COLWELL, R. K. 2000. A barrier runs through it… or maybe just a river. PNAS. 97: 13470 –13472.

CONDRATI, L.H. 2009. Padrões de distribuição e abundância de anuros em áreas ripárias e não ripárias de floresta de terra firme na Reserva Biológica do Uatumã - Amazônia Central. MSc Dissertation. Instituto Nacional de Pesquisas da Amazônia, Manaus.

CORNELL, H. V., AND J. H. LAWTON. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. J Anim Ecol. 61:1–12.

CORTÉS-GÓMEZ, A. M., F. CASTRO-HERRERA AND N. URBINA-CARDONA. 2013. Small changes in vegetation structure create great changes in amphibian ensembles in the Colombian Pacific rainforest. Tropical Conservation Science. 6: 749–769.

DEXTER, K. G., J.W. TERBORGH, AND C.W. CUNNINGHAM. 2012. Historical effects on beta diversity and community assembly in Amazonian trees. PNAS. 109: 7787–7792.

DNPM – Departamento Nacional da Produção Mineral – BRASIL. 1978. *Projeto RADAMBRASIL*—Levantamento dos recursos naturais. DNPM, Rio de Janeiro, Brazil.

FAITH, D. P., P.R. MINCHIN, AND L. BELBIN. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetation. 69: 57–68.

FEARNSIDE, P. M. 2014. Impacts of Brazil's Madeira River Dams: Unlearned lessons for hydroelectric development in Amazonia. Environ Sci Policy. 38: 164–172.

FOUQUET, A., B. P. NOONAN, M. T. RODRIGUES, N. PECH, A. GILLES, AND N. J. GEMMELL. 2012. Multiple Quaternary refugia in the eastern Guiana Shield revealed by comparative phylogeography of 12 frog species. Syst Biol. 61: 461–489.

FRAGA, R. DE, A. P. LIMA, AND W. E. MAGNUSSON. 2011. Mesoscale spatial ecology of a tropical snake assemblage: the width of riparian corridors in Central Amazonia. Herp Journal. 21: 51–57.

FUNK, W. C., J. P. CALDWELL, C. E. PEDEN, J. M. PADIAL, I. DE LA RIVA, AND D. C. CANNATELLA. 2007. Tests of biogeographic hypotheses for diversification in the Amazonian forest frog, Physalaemus petersi. Mol Phylogenet Evol. 44: 825–837.

GASCON, C., S. C. LOUGHEED, AND J. P. BOGART. 1996. Genetic and morphological variation in *Vanzolinius discodactylus*: a test of the river hypothesis of speciation. Biotropica. 28: 376–387.

GASCON, C., S. C. LOUGHEED, AND J. P. BOGART. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: a test of the riverine barrier hypothesis. Biotropica. 30: 104–119.

GASCON, C., J. R. MALCOLM, J. L. PATTON, M. N. F. DA SILVA, J. P. BOGART, S. C. LOUGHEED, C. A. PERES, S. NECKEL, AND P. T. BOAG. 2000. Riverine barriers and the geographic distribution of Amazonian species. PNAS. 97: 13672–13677.

HAYES, F. E. AND J. N. SEWLAL. 2004. The Amazon River as a dispersal barrier to passerine birds: Effects of river width, habitat and taxonomy. J Biogeogr. 31: 1809–1818.

HE, F., K. J. GASTON, E. F. CONNOR, AND D. S. SRIVASTAVA. 2005. The local-regional relationship: immigration, extinction and scale. Ecology. 86: 360–365.

HORBE, A. M. C., M. M. A., QUEIROZ, C. A. V. MOURA, AND M. A. G. TORO. 2013. Geoquímica das águas do médio e baixo Rio Madeira e seus principais tributários - Amazonas – Brasil. Acta Amazonica. 43: 489–504.

HUSTON, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86: 393–401.

JACKSON, D. A., P. R. PERES-NETO, AND J. D. OLDEN. 2001. What controls who is where in freshwater fish communities: the roles of biotic, abiotic, and spatial factors. Can J Fish Aquat Sci. 58:157–170.

KAEFER, I. L., B. M. TSUJI-NISHIKIDO, AND A. P. LIMA. 2012. Beyond the river: underlying determinants of population acoustic signal variability in Amazonian direct-developing *Allobates* (Anura: Dendrobatoidea). Acta Ethol. 5: 187–194.

KAEFER, I. L., B. M. TSUJI-NISHIKIDO, E. P. MOTA, I. P. FARIAS, AND A. P. LIMA. 2013. The early stages of speciation in Amazonian forest frogs: phenotypic conservatism despite strong genetic structure. Evol Biol. 40: 228–245.

KAHN, F. AND A. CASTRO. 1985. The palm community in a forest of central Amazonia, Brazil. Biotropica. 17: 210–216.

KEDDY, P. A. 1992. Assembly and response rules: Two goals for predictive community ecology. J Veg Sci. 3: 157–164.

KINUPP, V. F. AND W. E. MAGNUSSON. 2005. Spatial patterns in the understorey shrub genus *Psychotria* in central Amazonia: effects of distance and topography. J Trop Ecol. 21: 363–374.

LEITE, R. N. AND D. S. ROGERS. 2013. Revisiting Amazonian phylogeography: insights into diversification hypotheses and novel perspectives. Org Divers Evol. 13: 639–664.

LESCURE, J. P. AND R. BOULET. 1985. Relationships between soil and vegetation in a tropical rain forest in French Guiana. Biotropica. 17: 155–164.

LEVIN, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. Ecology. 73: 1943–1967.

LOUGHEED S. C., C. GASCON, D. A. JONES, J. P. BOGART, AND P. T. BOAG. 1999. Ridges and rivers: a test of competing hypotheses of Amazonian diversification using a dart-poison frog (*Epipedobates femoralis*). Proc. R. Soc. B Biol. Sci. 266: 1829–1835.

MAGNUSSON, W. E. 1997. Biogeography of Frogs: History as the Magic Bullet. J Biogeogr. 24: 251–252.

MAGNUSSON, W. E. AND G. MOURÃO. 2005. Estatística sem Matemática, 2ª ed. Londrina: Publisher Planta. 138p.

MAGNUSSON, W. E., R. B. N. PEZZINI, F. F. BACCARO, F. BERGALLO, H. PENHA, J. RODRIGUES, D. J. VERDADE, L. L. MARTINS, A. ALBERNAZ, A. L. HERO, J. M. LAWSON, B. E. CASTILHO, C. DRUCKER, D. FRANKLIN, E. MENDONÇA, F. COSTA, F. GALDINO, G. GUYER, C. ZUANON, J. VALE, J. SANTOS, J. L. C. LUIZÃO, R. C. CINTRA, R. I. BARBOSA, R. LISBOA; A. KOBLITZ, R. V. CUNHA, C. N. PONTES, AND A. R. MENDES. 2013. Biodiversidade e Monitoramento Ambiental Integrado: o sistema RAPELD na Amazônia. 1ª ed. Santo André - SP: Publisher Attema. 335p.

MENIN M., A. P. LIMA, W. E. MAGNUSSON, AND F. WALDEZ. 2007. Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns. J Trop Ecol. 23: 539–547.

MENIN, M., F. WALDEZ, AND A. P. LIMA. 2011. Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia. Herpetol J. 21: 255–261.

MONTAÑA, C., K. O. WINEMILLER, AND A. SUTTON. 2014. Intercontinental comparison of fish ecomorphology: null model tests of community assembly at the patch scale in rivers. Ecol Monogr. 84: 91–107.

MOUCHET, M. A., M. D. M. BURNS, A. M. GARCIA, J. P. VIEIRA, AND D. MOUILLOT. 2013. Invariant scaling relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos Lagoon estuary (Brazil): environmental filtering consistently overshadows competitive exclusion. Oikos. 122: 247–257.

MUNIZ, L. S., N. F. PANTOJA-JR, AND C. S. ALVES. 2013. Análise multitemporal da variabilidade de cotas fluviométricas do Rio Madeira - uma avaliação de danos sob extremas condições hidrológicas – Brasil. Anais XVI Simpósio Brasileiro de Sensoriamento Remoto – SBSR. 5761–5768 .

OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, R. G. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, AND H. WAGNER. 2010. Vegan: Community Ecology Package. R package version 1.17-1. Available in: http://CRAN.Rproject.org/package=vegan

PIANKA, E. R. 1973. The structure of lizard communities. Annu Rev Ecol Syst. 4: 53–74.

POMARA, L. Y., K. RUOKOLAINEN, AND K. R. YOUNG. 2013. Avian species composition across the Amazon River: the roles of dispersal limitation and environmental heterogeneity. J Biogeogr. 41: 784–796.

R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available in: http://www.R-project.org/.

RIBAS, C. C., A. ALEIXO, A. C. R. NOGUEIRA, C. Y. MIYAKI, AND J. CRACRAFT. 2011. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. P R Soc B. 279: 681–689.

RIBEIRO-JR, J. W., A. P. LIMA AND W. E. MAGNUSSON. 2012. The Effect of Riparian Zones on Species Diversity of Frogs in Amazonian Forests. Copeia. 3: 375–381.

RICKLEFS, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecol Lett. 7: 1–15.

RICKLEFS, R. E., AND S. S. RENNER. 2012. Global correlations in tropical tree species richness and abundance reject neutrality. Science 335: 464–467.

ROJAS-AHUMADA, D. P. 2010. Distribuição e abundância de anuros de floresta de terra firme na Fazenda Experimental da Universidade Federal do Amazonas – Amazônia Central. MSc Dissertation. Universidade Federal do Amazonas, Manaus.

ROJAS-AHUMADA, D. P., V. L. LANDEIRO, AND M. MENIN. 2012. Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. Austral Ecol. 37: 865–873.

RON, S. R. 2000. Biogeographic area relationships of lowland Neotropical rainforest on raw distributions of vertebrate groups. Biol J Linn Soc. 71: 379–402.

SILVA, J. M. C., A. B. RYLANDS, AND G. A. B. FONSECA. 2005. The fate of the Amazonian areas of endemism. Conserv Biol. 19: 689–694.

SIMÕES, P. I. 2010. Diversificação do complexo *Allobates femoralis* (Anura, Dendrobatidae) em florestas da Amazônia brasileira: desvendando padrões atuais e históricos. PhD Dissertation. Instituto Nacional de Pesquisas da Amazônia, Manaus.

SIMÕES, P. I., A. P. LIMA, W. E. MAGNUSSON, W. HÖDL, AND A. AMÉZQUITA. 2008. Acoustic and Morphological Differentiation in the Frog *Allobates femoralis*: Relationships with the Upper Madeira River and Other Potential Geological Barriers. Biotropica. 40: 607–614.

SIQUEIRA, C. C., D. VRCIBRADIC, P. NOGUEIRA-COSTA, A. R. MARTINS, L. DANTAS, V. L. R. GOMES, H. G. BERGALLO, AND C. F. D. ROCHA. 2014. Environmental parameters affecting the structure of leaf-litter frog (Amphibia: Anura) communities in tropical forests: A case study from an Atlantic Rainforest area in southeastern Brazil. Zoologia. 31: 147–152.

SOBRAL, F. L. AND M. V. CIANCIARUSO. 2012. Estrutura filogenética e funcional de assembleias: (re)montando a ecologia de comunidades em diferentes escalas espaciais. Biosci J. 28: 617–631.

SRIVASTAVA, D. S. 1999. Using local-regional richness plot to test for species saturation: pitfalls and potentials. J Anim Ecol. 68: 1–16.

TSUJI-NISHIKIDO, B. M., I. L. KAEFER, F. C. FREITAS, M. MENIN, & A. P. LIMA. 2012. Significant but not diagnostic: Differentiation through morphology and calls in the Amazonian frogs *Allobates nidicola* and *A. masniger*. Herpetol J. 22: 105–114.

VASCONCELOS, H. L., A. C. C. MACEDO, AND J. M. S. VILHENA. 2003. Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. Stud Neotrop Fauna E. 38: 115–124.

VELLEND, M. 2010. Conceptual synthesis in community ecology. Q Rev Biol. 85: 183–206.

VITT, L. J. AND J. P. CALDWELL. 1994. Resource utilization and guild structure of small vertebrates in the Amazon forest leaf litter. J Zool. 234: 463–476.

WALLACE, A. R. 1852. On the monkeys of the Amazon. P Zool Soc Lond. 20: 107–110.

WATLING J. I. 2005. Edaphically-biased distributions of amphibians and reptiles in a lowland tropical rainforest. Stud Neotrop Fauna E. 40: 15–21.

WOINARSKI J. C. Z., A. FISHER, AND D. MILNE. 1999. Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern territory, Australia. J Trop Ecol. 15: 381–98.

Tables

Table S1. Descriptive statistics of the environmental variables that composed the overall multiple regression model of the structure of diurnal frog assemblages. Variables were measured in 98 sample plots on the margins of the upper Madeira River, Rondônia, Brazil. VS, vegetation structure; EVC, extent of vegetation cover; Alt, altitude; SS soil structure (proportion of clay); SN, soil nutrients. Units and sampling protocols are given in Supplementary Material 1.

			VS	EVC	Alt	SS	SN
Plots	Right Bank	Mean	377.68	125.78	84.12	53.74	0.64
		Standard Deviation	82	31.56	14.27	10.79	0.24
		Maximum	579	202	128	70.7	1.56
		Minimum	221	72	63.8	18.1	0.31
	Left Bank	Mean	406.6	113.81	88.71	65.3	0.46
		Standard Deviation	89.32	44.61	21.82	8.46	0.17
		Maximum	613	347	172.55	77.7	0.82
		Minimum	247	60	71.98	47	0.18

Table S2. Species of diurnal frogs recorded from sample sites along the banks of the upper Madeira River, Rondônia, Brazil.

Family / Species
Aromobatidae
Allobates femoralis (Boulenger 1884)
Allobates hodli Simões, Lima & Farias 2010
Allobates nidicola (Caldwell & Lima 2003)
Allobates sp1
Allobates sp2
Allobates sp3
Allobates sp4
Allobates sp5
Dendrobatidae
Adelphobates quinquevittatus (Steindachner 1864)
Ameerega picta (Bibron 1838)
Ameerega trivittata (Spix 1824)
Leptodactylidae
Adenomera andreae (Müller 1923)
Adenomera hylaedactyla (Cope 1868)

Figure legends

FIGURE 1. Location of sample grids (black dots) on the Madeira River, Rondônia, Brazil. Grids from the right margin: Jirau-Right (JR), Jaci-Paraná (JP) and Morrinhos (MO). Grids from the left margin: Jirau-Left (JL), Ilha da Pedra (IP), Ilha do Bufalo (IB) and Teotônio (TE).

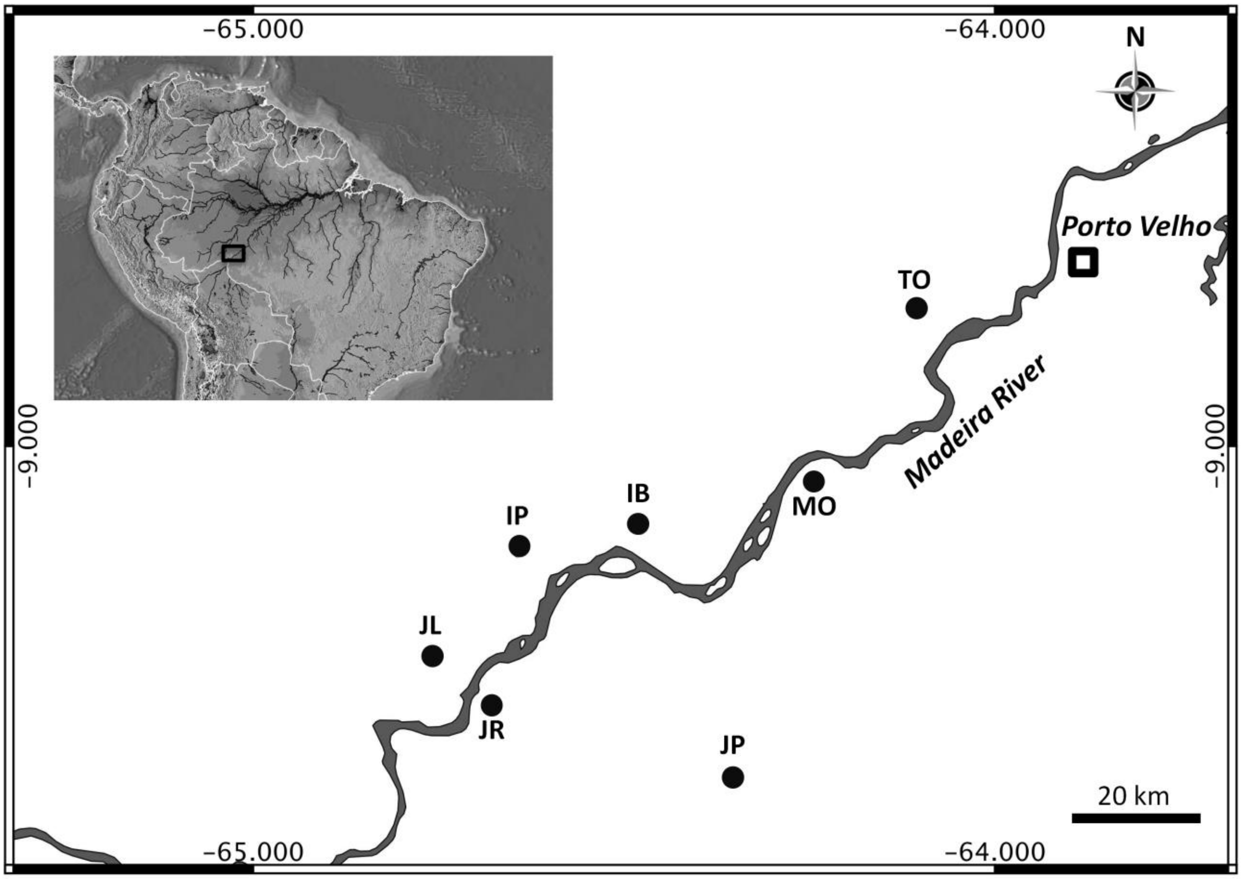
FIGURE 2. Relationship between the two axes generated after NMDS ordination, summarising 98 sample plots installed on the banks of the upper Madeira River, Rondônia, Brazil. Black circles represent study plots installed on the right bank. White circles represent study plots installed on the left bank.

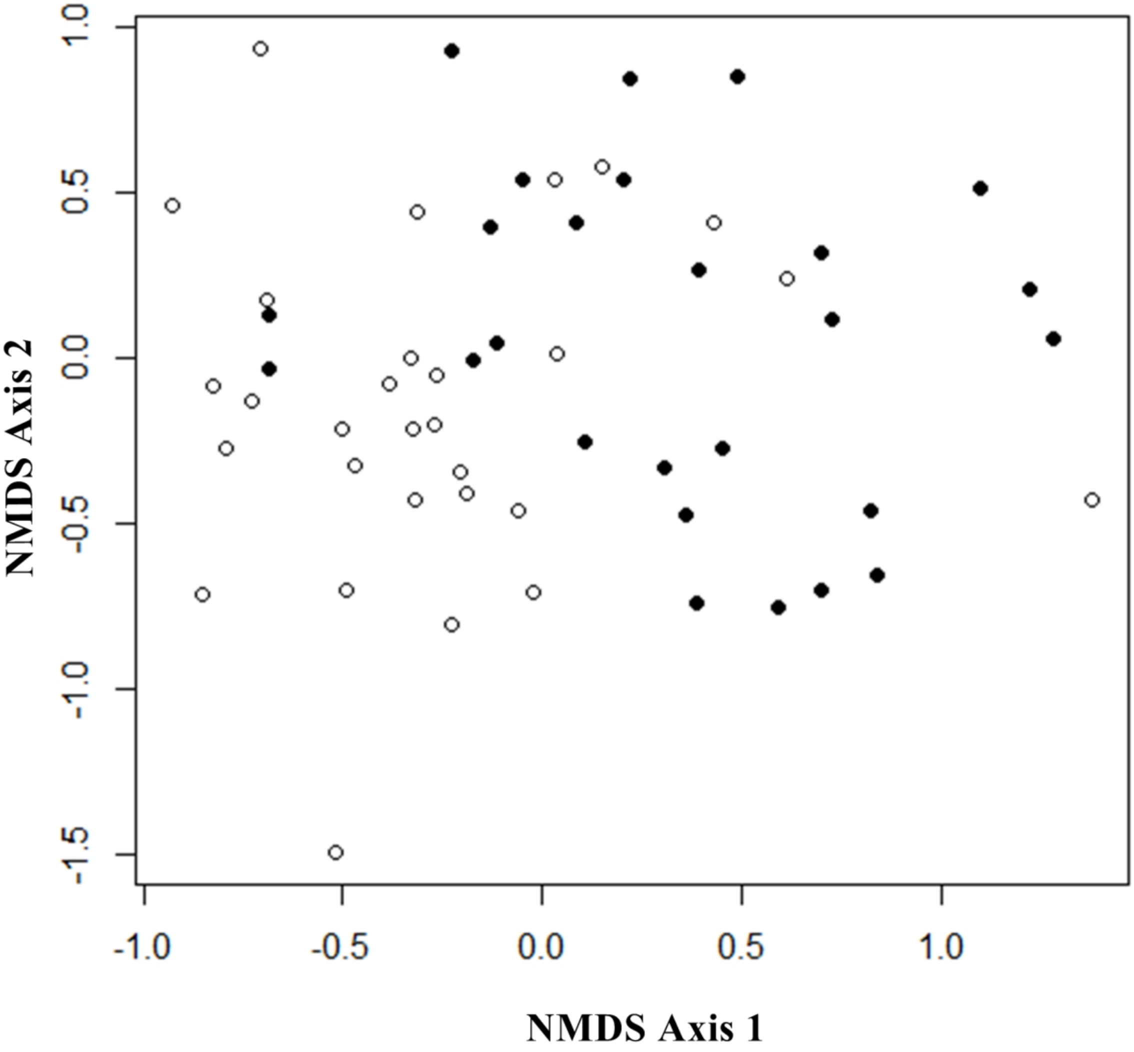
FIGURE 3. Ordination of species presence for diurnal leaflitter anuran relative to the margins of the upper Madeira River, Rondônia, Brazil.

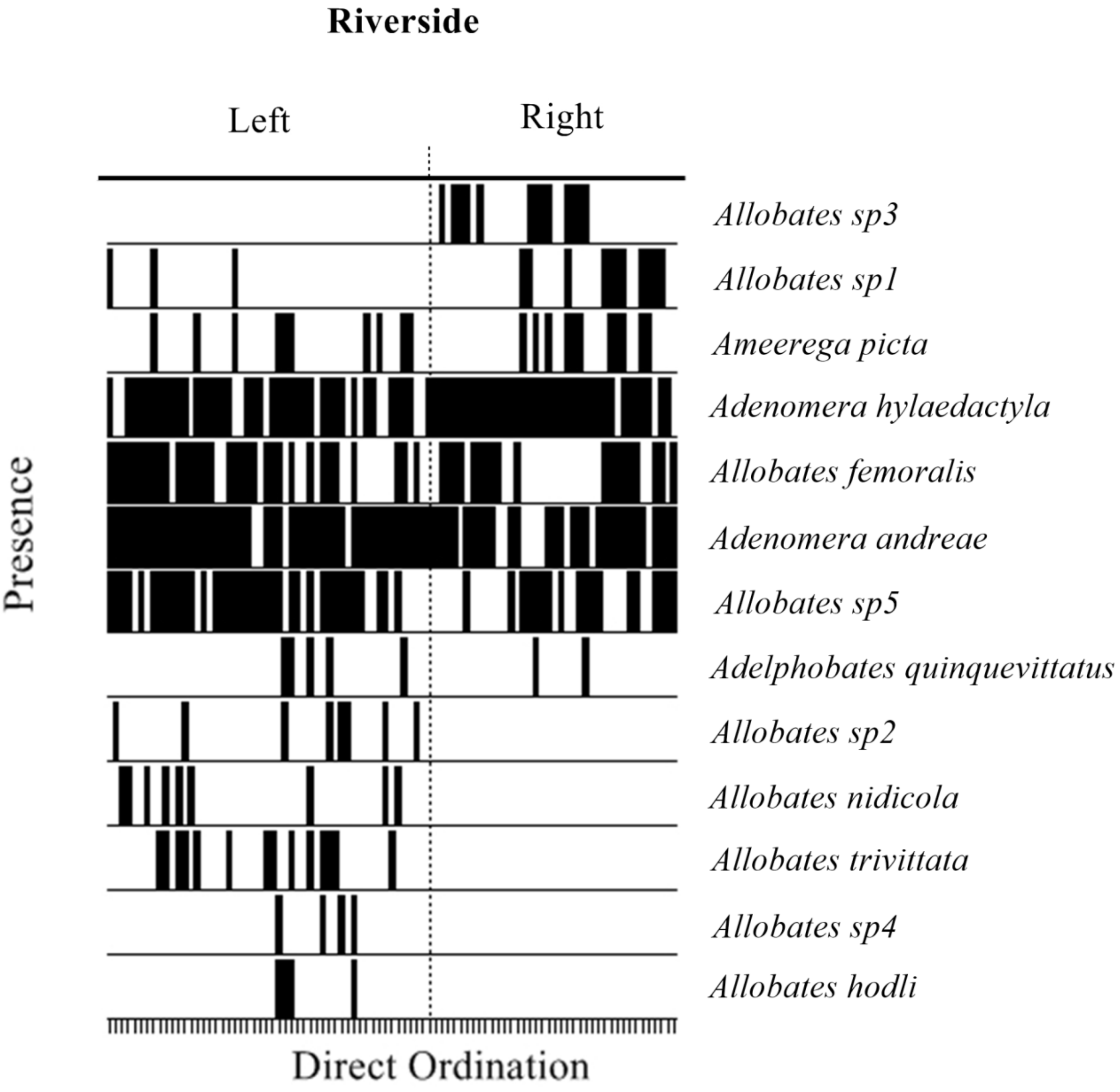
FIGURE 4. Ordination of encounter frequency for species of diurnal leaflitter anurans relative to a gradient of vegetation structure measured on the upper Madeira River, Rondônia, Brazil.

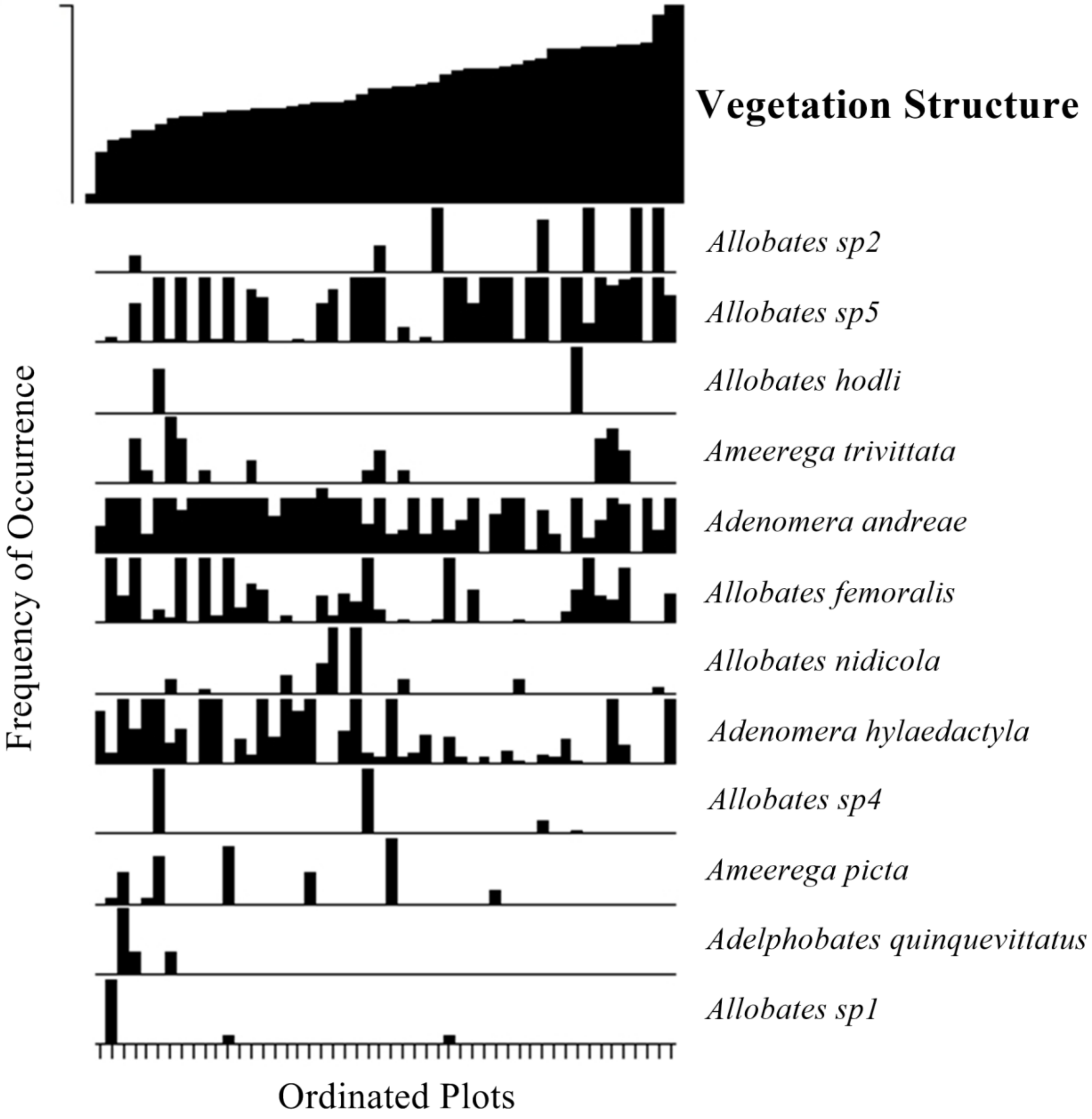
FIGURE 5. Variation in species composition (NMDS axis) of assemblages of diurnal anurans from different sites along the right bank of the upper Madeira River, Rondônia, Brazil.

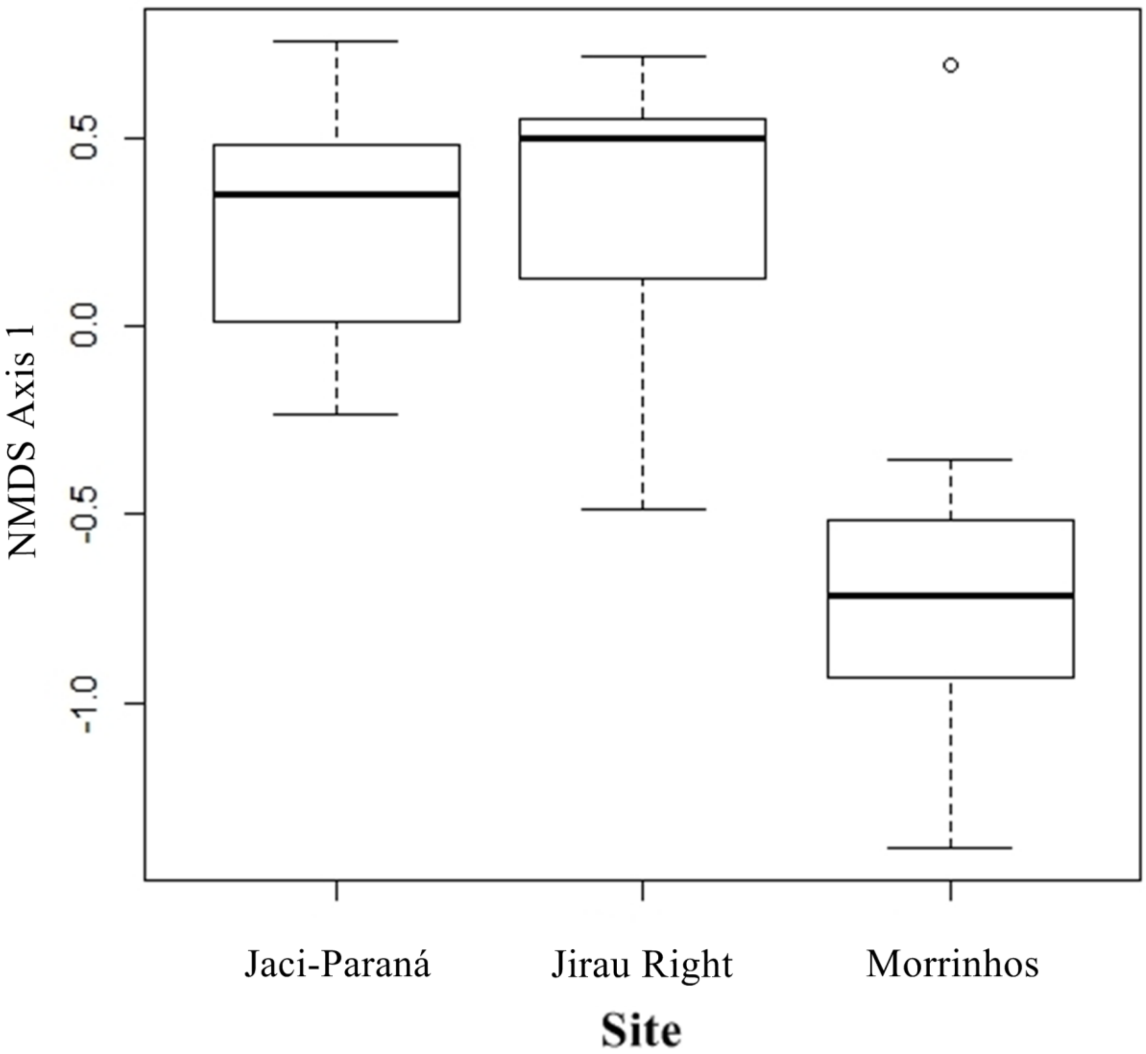
Figures


-65.000
-64.000
N
Porto Velho
TO
Madeira River
-9.000
-9.000
IB
IP
MO
JL
JR
JP
20 km
-65.000
-64.000


NMDS Axis 2
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
NMDS Axis 1


Riverside
Left
Right
Presence
Allobates sp3
Allobates sp1
Ameerega picta
Adenomera hylaedactyla
Allobates femoralis
Adenomera andreae
Allobates sp5
Adelphobates quinquevittatus
Allobates sp2
Allobates nidicola
Allobates trivittata
Allobates sp4
Allobates hodli
Direct Ordination


Vegetation Structure
Allobates sp2
Allobates sp5
Allobates hodli
Ameerega trivittata
Adenomera andreae
Allobates femoralis
Allobates nidicola
Adenomera hylaedactyla
Allobates sp4
Ameerega picta
Adelphobates quinquevittatus
Allobates sp1
Frequency of Occurrence
Ordinated Plots


NMDS Axis 1
0.5
0.0
-0.5
-1.0
Jaci-Paraná
Jirau Right
Morrinhos
Site

Appendix S1 - Supplementary Material

Environmental variables

The following environmental variables composed the overall multiple regression model of the structure of frog assemblages along the upper Madeira River: (1) vegetation structure - VS; (2) soil nutrients - SN; (3) soil structure (ratio of soil clay) - SS; (4) extent of vegetation cover - EVC; and (5) altitude – Alt

VEGETATION STRUCTURE.–The density sampling method used transects that varied in size depending on the size of the plant class being surveyed, as follows: (Transect 1) plants with a diameter at breast height (DBH) ≥ 1 cm were sampled in 1m-wide band to the left side of the centerline, for the entire length of the sample plot; (Transect 2) plants with DBH ≥ 10 cm were sampled in a 20 m wide band, with 10 m on either side of the plot center line. On the left, this band included Transects 1 and 3; (Transect 3) plants with DBH ≥ 30 cm were sampled in a range of 40 m wide, 20 m being on each side of the center line of the plot. On the left, this range overlapped with Transects 1 and 2, where all plants with DBH greater than or equal to 1 or 10 cm were measured. On the right side, this band includes Transect 2. More details of the plant data collection component are available at: http://ppbio.inpa.gov.br/sites/default/files/Estrutura_vegetacao.pdf. For statistical analyzes the total density of plants (sum values from Transects 1, 2 and 3 combined) per plot was used.

SOIL NUTRIENTS.–Soil pH was obtained from the effective H^+ ion concentration, determined with a combined electrode directly immersed in a soil solution diluted with distilled water at a 1:2.5ml ratio. Calcium, Magnesium and exchangeable Aluminum were extracted with KCl 1M. Exchangeable Al^{+3} was titrated with NaOH 0.025M using bromothymol blue as an indicator.

Ca^{+2} and Mg^{+2} levels were determined by atomic absorption spectrophotometry (AAS). Potassium and soil micronutrients (iron, zinc and manganese) was extracted with Mehlich I extraction solution (double-acid solution), consisting of a mixture of HCl 0.05M + H_2SO_4 0.0125M. The mL extract ratio was 1:10. K, Fe, Zn and Mn were determined by AAS. Available phosphorus was determined with a colorimetric spectrophotometer, using 3% ammonium molybdate and ascorbic acid. Using these values, formula was applied to the sum of bases, following the methods of Quesada et al. (2010), which allowed soil fertility in each plot to be inferred. For statistical analyzes the value for the sum of bases in each plot was used.

SOIL STRUCTURE (PROPORTION OF CLAY).–Soil samples were collected at six points on each plot (0, 50, 100, 150, 200 e 250 m along the plot length), at depths of 0 and 5 cm, once surface leaves had been removed. Samples were collected with a 5.5 cm diameter manual auger, stored in plastic bags and subsequently dried at room temperature and cleaned with tweezers, removing all pieces of leaf, root and charcoal. The material was processed and screened with a 2mm mesh sieve, then separated from other soil impurities to yield Fine Air-Dried Earth – FADE. Particle size analysis was made with composite samples (mixing sub-samples from soil obtained at 0, 50, 100, 150, 200 and 250 m) at INPA's Soil and Plant Science Laboratory. Particle size was estimated from an aliquot of 10 grams of soil by adding the chemical dispersant sodium pyrophosphate to separate soil particles. Organic matter was oxidized by heating with hydrogen peroxide. The proportion of clay was determined by dry weight of 20 ml of soil suspension. The coarse fraction (fine and coarse sand) were separated by sieving, dried in an oven (105 ° C for 24 hours) and weighed to obtain the respective percentages, following the PPBio methodology (http://ppbio.inpa.gov.br/knb/metacat). The average percentage of clay in the soil of each plot was used to represent particle size and this was then used in statistical analyzes.

EXTENT OF VEGETATION COVER.–The estimate of vegetation cover extent used the point plot method (Mantovani & Martins 1990), with samples every 2m from the start of the plot. Point plot locations were identified with a 50 m tape measure suspended 50 cm above the plot center line. All leaves or twigs touched by a positioned vertically 1.5 cm diameter metal rod 1.5 m in height, were recorded. For statistical analyzes the number of points that touched the metal rod at each point plot site was used.

ALTITUDE –A professional surveyor measured the altitude above sea level at the starting point of the plot. This was done because, to minimize variation in vegetation, soil type and drainage, each plot follows the local contour line and, consequently variation in altitude is minimal along its length. The value of the altitude of each plot was used for statistical analysis.

Literature Cited

MANTOVANI, W. AND F. R. MARTINS. 1990. O método de pontos. Acta Botânica Brasilica. 4: 95–122.

QUESADA, C. A., J. LLOYD, M. SCHWARZ, S. PATIÑO, T. R. BAKER, C. CZIMCZIK, N. M. FYLLAS, L. MARTINELLI, G. B. NARDOTO, J. SCHMERLER, A. J. B. SANTOS, M. G. HODNETT, R. HERRERA, F. J. LUIZÃO, A. ARNETH, G. LLOYD, N. DEZZEO, I. HILKE, I. KUHLMANN, M. RAESSLER, W. A. BRAND, H. GEILMANN, J. O. MORAES FILHO, F. P. CARVALHO, R. N. ARAUJO-FILHO, J. E. CHAVES, O. F. CRUZ-JUNIOR, T. P. PIMENTEL, AND R. Paiva. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences. 7: 1515–1541.

CONCLUSÕES GERAIS

Além de ilustrar os papéis de ambas as características históricas e ambientais sobre a estrutura de uma comunidade de anuros diurno em escalas regionais e locais, respectivamente, este estudo fornece um exemplo notável da heterogeneidade em escala precisa da biota amazônica rica em espécies. O padrão observado ao longo do alto Rio Madeira evoca a imagem da Amazônia como um "arquipélago de distintas áreas de endemismo separadas por grandes rios" (Silva et al., 2005). Juntamente com a alta proporção de espécies não descritas e crípticas em nossa amostra, este estudo chama a atenção para a necessidade de se caracterizar tanto a alfa como beta diversidade de anuros, a fim de estabelecer prioridades de conservação ao longo do Rio Madeira, uma região cada vez mais ameaçada pelo desmatamento e desenvolvimento econômico.

REFERÊNCIAS BIBLIOGRÁFICAS

AIBA, M., M. KATABUCHI, H. TAKAFUMI, S. S. MATSUZAKI, T. SASAKI, AND T. HIURA. 2013. Robustness of trait distribution metrics for community assembly studies under the uncertainties of assembly processes. Ecology. 94: 2873–2885.

ALGAR, A. C., J. T. KERR, AND D. L. CURRIE. 2011. Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. Ecology. 92: 903–914.

ALLMON, W. D. 1991. A plot study of forest floor litter frogs, Central Amazon, Brazil. J Trop Ecol. 7: 503–522.

ANTONELLI, A., A. QUIJADA-MASCAREÑAS, A. J. CRAWFORD, J. M. BATES, P. M. VELAZCO, AND W. WÜSTER. 2010. Molecular studies and phylogeography of Amazonian tetrapods and their relation to geological and climatic models. In C. Hoorn and F. P. Wesselingh (Eds.), Amazonia, landscape and species evolution, pp. 386–403. Blackwell Publishing, Oxford, UK.

AYRES, J. M., AND T. H. CLUTTON-BROCK. 1992. River boundaries and species range size in Amazonian primates. Am Nat. 140: 531–537.

BERNARDE, P. S. 2007. Ambientes e temporada de vocalização da anurofauna no Município de Espigão do Oeste, Rondônia, Sudoeste da Amazônia - Brasil (Amphibia: Anura). Biota Neotropica. 7: 87–92.

BERNARDE, P. S., AND M. N. C. KOKUBUM. 2009. Seasonality, age structure and reproduction of Leptodactylus (Lithodytes) lineatus (Anura, Leptodactylidae) in Rondônia state, southwestern Amazon, Brazil. Sér. Zool. 99: 368-372.

BERNARDE, P. S., M. N. C. KOKUBUM, R. A. MACHADO AND L. ANJOS. 1999. Uso de habitats naturais e antrópicos pelos anuros em uma localidade no Estado de Rondônia, Brasil (Amphibia: Anura). Acta Amazonica. 29: 555-562.

BROOKER, R. W., R. M. CALLAWAY, L. A. CAVIERES, Z. KIKVIDZE, C. J. LORTIE, R. MICHALET, F. I. PUGNAIRE, A. VALIENT-BANUET, AND T. G. WHITHAM. 2009. Don’t diss integration: a comment on Ricklefs’s disintegrating communities. Am Nat. 174: 919–921.

BROWN, J.H. 1995. Macroecology. University of Chicago Press, Chicago. 284p.

BUENO, A. S., R. S. BRUNO, T. P. PIMENTEL, T. M. SANAIOTTI, AND W. E. MAGNUSSON. 2012. The width of riparian habitats for understory birds in an Amazonian forest. Ecol Appl. 22: 722–734.

CAMPBELL, H. W. AND S. P. CHRISTMAN, 1982. Field techniques for herpetofaunal community analysis. In: N. J. Scott (Ed.). Herpetological Communities: a Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologist's League, pp. 193–200. U.S. Dept. of Interior, Fish and Wildlife Service - Wildlife Research Report, Washington, USA.

CASSEMIRO, F.A.S., AND A. A. PADIAL. 2008. Teoria Neutra da biodiversidade e biogeografia: aspectos teóricos, impactos na literatura e perspectivas. Oecol. Bras. 12: 706-719.

CAVALCANTE, M. M. A. 2012. Hidrelétricas do Rio Madeira - RO: território, tecnificação e meio ambiente. PhD Dissertation. Universidade Federal do Paraná, Curitiba.

CHAVE, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecol Lett. 16: 4–16.

CLARK, D. B., M. W PALMER, AND D. A. CLARK. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology. 80: 2662–2675.

COHN-HAFT, M. 2000. A case study in amazonian biogeography: Vocal and DNA sequence variation in *Hemitriccus flycatchers*. PhD Dissertation. Luisiana State University.

COLWELL, R. K. 2000. A barrier runs through it… or maybe just a river. PNAS. 97: 13470 –13472.

CONDRATI, L.H. 2009. Padrões de distribuição e abundância de anuros em áreas ripárias e não ripárias de floresta de terra firme na Reserva Biológica do Uatumã - Amazônia Central. MSc Dissertation. Instituto Nacional de Pesquisas da Amazônia, Manaus.

CORNELL, H. V., AND J. H. LAWTON. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. J Anim Ecol. 61:1–12.

CORTÉS-GÓMEZ, A. M., F. CASTRO-HERRERA AND N. URBINA-CARDONA. 2013. Small changes in vegetation structure create great changes in amphibian ensembles in the Colombian Pacific rainforest. Tropical Conservation Science. 6: 749–769.

DEXTER, K. G., J.W. TERBORGH, AND C.W. CUNNINGHAM. 2012. Historical effects on beta diversity and community assembly in Amazonian trees. PNAS. 109: 7787–7792.

DNPM – Departamento Nacional da Produção Mineral – BRASIL. 1978. *Projeto RADAMBRASIL*—Levantamento dos recursos naturais. DNPM, Rio de Janeiro, Brazil.

ERNST, R., AND M. O. RÖDEL. 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. Ecology. 86: 3111–3118.

FAITH, D. P., P.R. MINCHIN, AND L. BELBIN. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetation. 69: 57–68.

FOUQUET, A., B. P. NOONAN, M. T. RODRIGUES, N. PECH, A. GILLES, AND N. J. GEMMELL. 2012. Multiple Quaternary refugia in the eastern Guiana Shield revealed by comparative phylogeography of 12 frog species. Syst Biol. 61: 461–489.

FUNK, W. C., J. P. CALDWELL, C. E. PEDEN, J. M. PADIAL, I. DE LA RIVA, AND D. C. CANNATELLA. 2007. Tests of biogeographic hypotheses for diversification in the Amazonian forest frog, Physalaemus petersi. Mol Phylogenet Evol. 44: 825–837.

GASCON, C., J. R. MALCOLM, J. L. PATTON, M. N. F. DA SILVA, J. P. BOGART, S. C. LOUGHEED, C. A. PERES, S. NECKEL, AND P. T. BOAG. 2000. Riverine barriers and the geographic distribution of Amazonian species. PNAS. 97: 13672–13677.

GASCON, C., S. C. LOUGHEED, AND J. P. BOGART. 1996. Genetic and morphological variation in *Vanzolinius discodactylus*: a test of the river hypothesis of speciation. Biotropica. 28: 376–387.

GASCON, C., S. C. LOUGHEED, AND J. P. BOGART. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: a test of the riverine barrier hypothesis. Biotropica. 30: 104–119.

HAYES, F. E. AND J. N. SEWLAL. 2004. The Amazon River as a dispersal barrier to passerine birds: Effects of river width, habitat and taxonomy. J Biogeogr. 31: 1809–1818.

HE, F., K. J. GASTON, E. F. CONNOR, AND D. S. SRIVASTAVA. 2005. The local-regional relationship: immigration, extinction and scale. Ecology. 86: 360–365.

HORBE, A. M. C., M. M. A., QUEIROZ, C. A. V. MOURA, AND M. A. G. TORO. 2013. Geoquímica das águas do médio e baixo Rio Madeira e seus principais tributários - Amazonas – Brasil. Acta Amazonica. 43: 489–504.

Hu, X. S., F. L. He, and S. P. Hubbell. 2006. Neutral theory in macroecology and population genetics. Oikos. 113: 548-556.

HUSTON, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86: 393–401.

JACKSON, D. A., P. R. PERES-NETO, AND J. D. OLDEN. 2001. What controls who is where in freshwater fish communities: the roles of biotic, abiotic, and spatial factors. Can J Fish Aquat Sci. 58:157–170.

KAEFER, I. L., B. M. TSUJI-NISHIKIDO, AND A. P. LIMA. 2012. Beyond the river: underlying determinants of population acoustic signal variability in Amazonian direct-developing *Allobates* (Anura: Dendrobatoidea). Acta Ethol. 5: 187–194.

KAEFER, I. L., B. M. TSUJI-NISHIKIDO, E. P. MOTA, I. P. FARIAS, AND A. P. LIMA. 2013. The early stages of speciation in Amazonian forest frogs: phenotypic conservatism despite strong genetic structure. Evol Biol. 40: 228–245.

KAHN, F. AND A. CASTRO. 1985. The palm community in a forest of central Amazonia, Brazil. Biotropica. 17: 210–216.

KEDDY, P. A. 1992. Assembly and response rules: Two goals for predictive community ecology. J Veg Sci. 3: 157–164.

KELLER, A., M. RÖDEL, K. E. LINDENMAIR, AND T. U. GRAFE. 2009. The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. Journal of Animal Ecology, 78: 305-314.

KINUPP, V. F. AND W. E. MAGNUSSON. 2005. Spatial patterns in the understorey shrub genus *Psychotria* in central Amazonia: effects of distance and topography. J Trop Ecol. 21: 363–374.

LEITE, R. N. AND D. S. ROGERS. 2013. Revisiting Amazonian phylogeography: insights into diversification hypotheses and novel perspectives. Org Divers Evol. 13: 639–664.

LESCURE, J. P. AND R. BOULET. 1985. Relationships between soil and vegetation in a tropical rain forest in French Guiana. Biotropica. 17: 155–164.

LEVIN, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. Ecology. 73: 1943–1967.

LOUGHEED S. C., C. GASCON, D. A. JONES, J. P. BOGART, AND P. T. BOAG. 1999. Ridges and rivers: a test of competing hypotheses of Amazonian diversification using a dart-poison frog (*Epipedobates femoralis*). Proc. R. Soc. B Biol. Sci. 266: 1829–1835.

MAGNUSSON, W. E. 1997. Biogeography of Frogs: History as the Magic Bullet. J Biogeogr. 24: 251–252.

MAGNUSSON, W. E. AND G. MOURÃO. 2005. Estatística sem Matemática, 2ª ed. Londrina: Publisher Planta. 138p.

MAGNUSSON, W. E., R. B. N. PEZZINI, F. F. BACCARO, F. BERGALLO, H. PENHA, J. RODRIGUES, D. J. VERDADE, L. L. MARTINS, A. ALBERNAZ, A. L. HERO, J. M. LAWSON, B. E. CASTILHO, C. DRUCKER, D. FRANKLIN, E. MENDONÇA, F. COSTA, F. GALDINO, G. GUYER, C. ZUANON, J. VALE, J. SANTOS, J. L. C. LUIZÃO, R. C. CINTRA, R. I. BARBOSA, R. LISBOA; A. KOBLITZ, R. V. CUNHA, C. N. PONTES, AND A. R. MENDES. 2013. Biodiversidade e Monitoramento Ambiental Integrado: o sistema RAPELD na Amazônia. 1ª ed. Santo André - SP: Publisher Attema. 335p.

MANTOVANI, W. AND F. R. MARTINS. 1990. O método de pontos. Acta Botânica Brasilica. 4: 95–122.

MENIN M., A. P. LIMA, W. E. MAGNUSSON, AND F. WALDEZ. 2007. Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns. J Trop Ecol. 23: 539–547.

MENIN, M., F. WALDEZ, AND A. P. LIMA. 2011. Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia. Herpetol J. 21: 255–261.

MONTAÑA, C., K. O. WINEMILLER, AND A. SUTTON. 2014. Intercontinental comparison of fish ecomorphology: null model tests of community assembly at the patch scale in rivers. Ecol Monogr. 84: 91–107.

MOUCHET, M. A., M. D. M. BURNS, A. M. GARCIA, J. P. VIEIRA, AND D. MOUILLOT. 2013. Invariant scaling relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos Lagoon estuary (Brazil): environmental filtering consistently overshadows competitive exclusion. Oikos. 122: 247–257.

MUNIZ, L. S., N. F. PANTOJA-JR, AND C. S. ALVES. 2013. Análise multitemporal da variabilidade de cotas fluviométricas do Rio Madeira - uma avaliação de danos sob extremas condições hidrológicas – Brasil. Anais XVI Simpósio Brasileiro de Sensoriamento Remoto – SBSR. 5761–5768 .

OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, R. G. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, AND H. WAGNER. 2010. Vegan: Community Ecology Package. R package version 1.17-1. Available in: http://CRAN.Rproject.org/package=vegan

PARRIS, K. M. 2004. Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. Ecography. 27: 392-400.

PIANKA, E. R. 1973. The structure of lizard communities. Annu Rev Ecol Syst. 4: 53–74.

POMARA, L. Y., K. RUOKOLAINEN, AND K. R. YOUNG. 2013. Avian species composition across the Amazon River: the roles of dispersal limitation and environmental heterogeneity. J Biogeogr. 41: 784–796.

QUESADA, C. A., J. LLOYD, M. SCHWARZ, S. PATIÑO, T. R. BAKER, C. CZIMCZIK, N. M. FYLLAS, L. MARTINELLI, G. B. NARDOTO, J. SCHMERLER, A. J. B. SANTOS, M. G. HODNETT, R. HERRERA, F. J. LUIZÃO, A. ARNETH, G. LLOYD, N. DEZZEO, I. HILKE, I. KUHLMANN, M. RAESSLER, W. A. BRAND, H. GEILMANN, J. O. MORAES FILHO, F. P. CARVALHO, R. N. ARAUJO-FILHO, J. E. CHAVES, O. F. CRUZ-JUNIOR, T. P. PIMENTEL, AND R. Paiva. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences. 7: 1515–1541.

R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available in: http://www.R-project.org/.

RIBAS, C. C., A. ALEIXO, A. C. R. NOGUEIRA, C. Y. MIYAKI, AND J. CRACRAFT. 2011. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. P R Soc B. 279: 681–689.

RIBEIRO-JR, J. W., A. P. LIMA AND W. E. MAGNUSSON. 2012. The Effect of Riparian Zones on Species Diversity of Frogs in Amazonian Forests. Copeia. 3: 375–381.

Ricklefs, R. E. & Schluter, D. 1993. Species diversity: regional and historical influences. Pp 350-363. In: R. E. Ricklefs and D. Schluter, (eds.), Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago. 432p.

RICKLEFS, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecol Lett. 7: 1–15.

RICKLEFS, R. E., AND S. S. RENNER. 2012. Global correlations in tropical tree species richness and abundance reject neutrality. Science 335: 464–467.

RODRIGUES, D. J. 2006. Influência de fatores bióticos e abióticos na distribuição temporal e espacial de girinos de comunidades de poças temporárias em 64 km^2 de floresta de terra firme na Amazônia Central. PhD Dissertation. Instituto Nacional de Pesquisas da Amazônia, Manaus.

ROJAS-AHUMADA, D. P. 2010. Distribuição e abundância de anuros de floresta de terra firme na Fazenda Experimental da Universidade Federal do Amazonas – Amazônia Central. MSc Dissertation. Universidade Federal do Amazonas, Manaus.

ROJAS-AHUMADA, D. P., V. L. LANDEIRO, AND M. MENIN. 2012. Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. Austral Ecol. 37: 865–873.

RON, S. R. 2000. Biogeographic area relationships of lowland Neotropical rainforest on raw distributions of vertebrate groups. Biol J Linn Soc. 71: 379–402.

SANTOS, T.G., T. S. Vasconcelos, and C. F. B. Haddad. 2012. The Role of Environmental Heterogeneity in Maintenance of Anuran Amphibian Diversity of the

Brazilian Mesophytic Semideciduous Forest. In: Tropical Forests. Sudarshana, P.; Nageswara-Rao, M. & Soneji, J. R..(Org.). Rijeka: InTech. 119-138 p.

SILVA, F. R., C. P. Candeira, and D. C. Rossa-Feres. 2012. Dependence of anuran diversity on environmental descriptors in farmland ponds. Biodiversity Conservation. 21: 1411-1424.

SILVA, J. M. C., A. B. RYLANDS, AND G. A. B. FONSECA. 2005. The fate of the Amazonian areas of endemism. Conserv Biol. 19: 689–694.

SILVA, R.A., I. A. MARTINS, AND D. C. ROSSA-FERES. 2011. Environmental heterogeneity: Anuran diversity in homogeneous environments. Zoologia. 28: 610-618.

SIMÕES, P. I. 2010. Diversificação do complexo *Allobates femoralis* (Anura, Dendrobatidae) em florestas da Amazônia brasileira: desvendando padrões atuais e históricos. PhD Dissertation. Instituto Nacional de Pesquisas da Amazônia, Manaus.

SIMÕES, P. I., A. P. LIMA, W. E. MAGNUSSON, W. HÖDL, AND A. AMÉZQUITA. 2008. Acoustic and Morphological Differentiation in the Frog *Allobates femoralis*: Relationships with the Upper Madeira River and Other Potential Geological Barriers. Biotropica. 40: 607–614.

SIQUEIRA, C. C., D. VRCIBRADIC, P. NOGUEIRA-COSTA, A. R. MARTINS, L. DANTAS, V. L. R. GOMES, H. G. BERGALLO, AND C. F. D. ROCHA. 2014. Environmental parameters affecting the structure of leaf-litter frog (Amphibia: Anura) communities in tropical forests: A case study from an Atlantic Rainforest area in southeastern Brazil. Zoologia. 31: 147–152.

SOBRAL, F. L. AND M. V. CIANCIARUSO. 2012. Estrutura filogenética e funcional de assembleias: (re)montando a ecologia de comunidades em diferentes escalas espaciais. Biosci J. 28: 617–631.

SRIVASTAVA, D. S. 1999. Using local-regional richness plot to test for species saturation: pitfalls and potentials. J Anim Ecol. 68: 1–16.

TSUJI-NISHIKIDO, B. M., I. L. KAEFER, F. C. FREITAS, M. MENIN, & A. P. LIMA. 2012. Significant but not diagnostic: Differentiation through morphology and calls in the Amazonian frogs *Allobates nidicola* and *A. masniger*. Herpetol J. 22: 105–114.

VASCONCELOS, H. L., A. C. C. MACEDO, AND J. M. S. VILHENA. 2003. Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. Stud Neotrop Fauna E. 38: 115–124.

VASCONCELOS, T. S. AND D. C. ROSSA-FERES. 2008. Habitat heterogeneity and use of physical and acoustic space in anuran communities in Southeastern Brazil. Phyllomedusa. 7: 127-142.

VASCONCELOS, T. S., T. G. SANTOS, D. C. ROSSA-FERES, AND C. F. B. HADDAD. 2009. Influence of the environmental heterogeneity of breedin ponds on anuran assemblages from southeastern Brazil. Can. J. of Zool. 87: 699-707.

VELLEND, M. 2010. Conceptual synthesis in community ecology. Q Rev Biol. 85: 183–206.

VITT, L. J. AND J. P. CALDWELL. 1994. Resource utilization and guild structure of small vertebrates in the Amazon forest leaf litter. J Zool. 234: 463–476.

WALLACE, A. R. 1852. On the monkeys of the Amazon. P Zool Soc Lond. 20: 107–110.

WATLING J. I. 2005. Edaphically-biased distributions of amphibians and reptiles in a lowland tropical rainforest. Stud Neotrop Fauna E. 40: 15–21.

WOINARSKI J. C. Z., A. FISHER, AND D. MILNE. 1999. Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern territory, Australia. J Trop Ecol. 15: 381–98.

ZHOU, S. AND D. ZHANG. 2008. Neutral theory in community ecology. Frontiers of Biology in China. 3: 1-8.