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Turnover de anuros da Amazônia, perspectivas em multi escalas e habitats

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Tese de doutorado apresentado ao Programa de Pós-Graduação em Zoologia da Universidade Federal do Pará/Museu Paraense Emílio Goeldi.

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Eu sei um pouco de muita coisa,

mas muito mesmo eu não sei de quase nada!

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Sumário

RESUMO GERAL

Entender os processos envolvidos na distribuição espacial das espécies e as razões que levam a dissimilaridades na composição entre locais (turnover) têm sido objeto de diversos estudos em diferentes escalas e hábitats. Neste estudo, investigamos os fatores responsáveis pelo *turnover* de anfíbios anuros sob três diferentes perspectivas. No primeiro capítulo dessa tese, intitulado "**Anuran beta diversity in a mosaic anthropogenic landscape in transitional Amazon**", nós testamos de que forma cinco diferentes ambientes, classificados de acordo com a pressão antrópica, podem estruturar o *turnover* de anuros. As unidades amostrais para este primeiro capítulo estão localizadas em um ecótono entre os biomas Amazônia e Cerrado, numa região denominada como arco do desflorestamento. Observamos que a conversão de áreas florestadas (matas ciliares) em ambientes mais abertos (monocultura de grãos e seringal) resulta na mudança da composição de espécies original e na diminuição do turnover, algo que podemos chamar de homogeneização da fauna. Porém, a ideia de mudança no *turnover* ao se comparar ambientes estruturalmente diferentes não é novidade, ainda mais quando apresentam graus de degradação tão distintos como os encontrados na área de estudo. Dessa forma, no segundo capítulo da tese, "**Species turnover in Amazonian frogs: Low predictability and large differences among terra firme forests**", buscamos identificar o quanto variações ambientais e espaciais contribuem para a estruturação das comunidades em florestas de terra firme na Amazônia. As unidades amostrais para este segundo capítulo estão localizadas em três unidades de conservação da Amazônia brasileira (Florestas Nacionais do Amapá, Caxiuanã e Tapajós). Detectamos que, embora sejam áreas em teoria similares (terra firme), cada uma das comunidades responde a um conjunto específico de variáveis ambientais. Ao testarmos os fatores estruturando o *turnover* entre escalas distintas, observamos que tanto a porção explicada pelo ambiente quanto pelo espaço apresentaram maior poder de explicação (r^2) em escalas regionais quando comparados com cada uma das localidades (escala local). Outro resultado interessante foi que o componente espacial não apresentou influência significativa sobre a comunidade de Caxiuanã, onde somente 3% do *turnover* foi explicado por qualquer um dos fatores ambientais medidos. Por último, o terceiro capítulo intitulado "**How differences in anuran reproductive modes can affect their turnover: comparing scales and**

habitat", aborda como anuros com diferentes atributos reprodutivos respondem a variações ambientais e espaciais, comparando esses processos em florestas de terra firme e várzea. Adicionalmente, avaliamos a probabilidade de ocorrência das espécies mais comuns ao longo dos gradientes ambientais mensurados. As unidades amostrais deste capítulo estão localizadas em três áreas de floresta de terra firme (as mesmas do capítulo 2) e duas áreas de várzea (Reserva de Desenvolvimento Sustentável de Mamirauá e Amanã). Espécies com oviposição aquática foram predominantes nas áreas de várzea, enquanto houve maior proporção de ovipositores na vegetação em Caxiuanã e mais espécies com reprodução terrestre no Amapá e Tapajós, quando comparadas com as demais áreas. Ao dividir as espécies de acordo com seus modos reprodutivos, padrões mais claros de resposta puderam ser observados. Podemos afirmar ainda que mudanças nas características ambientais aparecem como importantes estruturadoras do *turnover* em diferentes escalas, enquanto a distância espacial é mais evidente em escalas maiores. Assim, podemos concluir que em áreas impactadas o *turnover* entre as comunidades diminui pela homogeneização da fauna, em decorrência da conversão de florestas em áreas antropizadas. Por outro lado, observamos também que mesmo em áreas dentro de uma mesma classificação fitofisionomica e sem distúrbios antrópicos, há grandes diferenças nos padrões de partição do *turnover*, que podem ser atribuídos a conjuntos de fatores ambientais e espaciais específicos de cada área, além de espécies com diferentes atributos reprodutivos.

ABSTRACT

Understanding the processes involved in the species spatial distribution and the reasons leading to compositional dissimilarities among sites (turnover) have been studied on different scales and habitats. In the present study, we investigated the factors affecting frogs turnover from three different perspectives. In our first chapter of this thesis, entitled "**Anuran beta diversity in the mosaic anthropogenic landscape in transitional Amazon**", we tested how five environments, classified according to their human pressure, can structure frogs turnover. Sampling units (SU) on this first chapter are located in a ecotone between the Amazon and Cerrado biomes, also known as "Arc of deforestation". We observed that the conversion of forested areas (riparian forests) in open environments (monoculture of grains and rubber tree) result substitution of the original species and low turnover rates, something we can call faunal homogenization. However, the concept that turnover may change over structurally different environments is not new, specially if they have a strong degradation gradient, as found in the study area. Thus, in the second chapter of this thesis, "**Species turnover in Amazonian frogs: Low predictability and large differences among terra firme forests**", we seek to identify how environmental and spatial variation contribute to structure communities in well preserved *terra-firme* forests in Amazonia. The SU for this second chapter are located over three conservation units (National Forests of Amapá, Caxiuanã and Tapajós). We observed that, despite considered within the same class (*terra firme*), each community responds to a singular set of environmental variables. Testing the factors influencing species turnover over different scales, we observed that both the portion explained by environment and space had greater explanatory power (r^2) in regional scales when compared within each of the areas (local scale). Another interesting result was that the spatial component showed no significant influence on Caxiuanã community, where only 3% of turnover was accounted for by any of the measured environmental factors. Finally, on third chapter titled "**How differences in anuran reproductive modes can affect their turnover: Comparing scales and habitats**", we discusses how frogs with different reproductive modes respond to environmental and spatial variations, comparing these processes in *terra firme* and *varzea* forests. Additionally, we evaluated species probability of occurrence along measured environmental gradients. The SU in this chapter are located in three areas of *terra firme*

forest (the same as in Chapter 2) and two areas of *varzea* (Sustainable Development Reserve Mamirauá and Amana). Species with aquatic oviposition were prevalent in *varzea*, while there was a higher proportion species laying on the vegetation in Caxiuanã and more species with terrestrial reproduction in Amapá and Tapajós when compared to the other areas. By dividing the species according to their reproductive modes, clearer response patterns were observed. Also, we can assert that changes in environmental characteristics appear as major turnover driver and are important in all scales, while the spatial distance is more evident at larger scales. Thus, we can conclude that in disturbed areas faunal homogenization decreases species turnover, due to the conversion of forests into open and less heterogeneous areas. Moreover, we also observed that even in areas within the same classification and without human disturbances, there are great differences in turnover partitioning patterns, which can be assigned to a specific set spatial and environmental factors inherent to each area, in addition to species with different reproductive modes.

INTRODUÇÃO GERAL

A busca constante por processos que levam a padrões de distribuição das espécies no tempo e no espaço vem intrigando cientistas há mais de meio século (Wittaker 1960; Angermeier & Winston 1998, Zuquim *et al.* 2012, Tuomisto *et al.* 2014). Desde que o conceito foi difundido por Whittaker (1960), a mudança na composição de espécies entre locais tem recebido diferentes definições (Tuomisto 2010a) e diferentes mecanismos tem sido desenvolvidos para mensurar esse efeito (Tuomisto 2010b). Atualmente, o termo *turnover* tem sido usado para descrever a dissimilaridade na composição de espécies ao longo de um gradiente espacial. Em florestas tropicais, ainda não existe um consenso sobre quais fatores podem influenciar o *turnover*, isto porque os resultados encontrados em diferentes estudos podem apresentar conclusões divergentes dependendo do local, da escala e do grupo taxonômico investigado (Novotny *et al.* 2007, Dahl *et al.* 2009, Qian & Ricklefs 2012).

Diferenças no tipo de hábitat (Von May *et al.* 2010) e/ou no grau de perturbação (Bitar *et al.* 2015) em uma determinada área podem afetar diretamente o padrão de substituição das espécies. Modificações no ambiente podem levar a um efeito homogeneizador, reduzindo a complexidade de hábitats e, por sua vez, a riqueza de espécies (Hazell *et al.* 2001, Olden *et al.* 2004, Conte & Machado 2005, Vasconcelos & Rossa-Feres 2005). Para anfíbios, assim como para vários outros grupos de vertebrados, a perda de hábitat e fragmentação ao longo das últimas décadas são apontados como principais fatores determinantes do declínio e extinção de espécies em todo o mundo, levando ao que conhecemos como "crise da biodiversidade" (Beebee 1996, Alford & Richards 1999, Houlahan *et al.* 2000, Bielby *et al.* 2008). Para a Amazônia brasileira, o desmatamento vem se intensificando em ritmo acelerado, com um aumento de 70% apenas no último ano (Fonseca *et al.* 2014). Dentro deste cenário, é fundamental entendermos o que determina a distribuição das espécies e o que estamos tentando conservar. Entender como alterações ambientais influenciam o *turnover* de espécies em ambientes alterados na Amazônia, além de estabelecer comparações com áreas preservadas, pode nos fornecer pistas do que poderá ocorrer no futuro com as comunidades de regiões ainda preservadas.

Quando falamos em conservação, não queremos apenas entender as mudanças que já ocorreram em um ambiente, mas principalmente compreender os processos que mantêm os padrões que estamos tentando identificar e posteriormente conservar. Assim, além de entendermos como os impactos antrópicos podem gerar diferentes padrões de distribuição das espécies, temos que buscar entender quais os fatores responsáveis pelos padrões observados em ambientes ainda preservados. Sabemos que a distribuição das espécies pode ser influenciada por vários fatores, tais como parâmetros ambientais (ex. tipo de hábitat e gradientes ambientais) e espaciais (efeito da distância geográfica), e que o entendimento do efeito desses componentes pode ser uma importante ferramenta no entendimento das razões que levam à essa dissimilaridade composicional (Tuomisto *et al.* 2003).

Quanto aos parâmetros ambientais e seguindo as premissas da teoria do nicho, é intuitivo pensarmos que ambientes ecologicamente parecidos, que compartilham características ambientais semelhantes (e.g. tipo de vegetação, estrutura da paisagem e heterogeneidade de hábitat), devem apresentar uma composição de espécies mais similares quando comparadas com ambientes mais dissimilares (Grinnel 1917, Hutchinson 1957, Whittaker 1960). De acordo com essa teoria, as condições do ambiente e a relação entre as espécies são responsáveis pelos padrões de composição e diversidade observados em uma comunidade. Por outro lado, baseado nas premissas da teoria neutra da biodiversidade, padrões de composição e diversidade das espécies podem também ser resultado de fatores estocásticos, especialmente ao se considerar que todas as espécies possuem igual probabilidade de ocuparem um hábitat (Hubbell 2001). Nesse contexto, a habilidade de dispersão das espécies seria um importante fator estruturando a composição de um determinado local (McGill *et al.* 2006), de modo que quanto mais distantes dois ambientes entre si, menos similar será sua composição de espécies (espacialmente estruturados). Ao se ter isso em mente, poderíamos dizer que quanto menor a habilidade de dispersão das espécies em uma região, maior deverá ser o *turnover* de espécies ao longo do gradiente espacial (Gastón & Chown 2005, Soininen *et al.* 2007), enquanto comunidades com espécies com maior habilidade de dispersão deverão apresentar menor *turnover*, pois sua biota seria mais homogênea (Hubbell 2001).

Identificar a importância relativa de cada um dos parâmetros ambientais e espaciais sobre o *turnover* pode nos ajudar a esclarecer os processos que mantém os padrões de distribuição das espécies e a diversidade observados atualmente, tanto em ambientes preservados quanto impactados. Porém, é importante ressaltar que para um mesmo grupo taxonômico, tanto o ambiente quanto o espaço podem apresentar pesos de importância diferentes para determinar mudanças na composição de espécies. Isto porque: (i) a habilidade de dispersão das espécies é um atributo funcional espacialmente estruturado, (ii) podemos ter autocorrelação espacial nas variáveis ambientais, (iii) ou ainda uma combinação de ambos. Portanto, ao se medir a importância relativa das frações espaço e ambiente sobre o *turnover*, deve-se considerar sempre que a escala de observação e os parâmetros ambientais medidos como preditores devem ser escolhidos de acordo com o grupo taxonômico usado como modelo (Qian & Ricklefs 2012). Isto porque, o modo como as espécies percebem e respondem ao ambiente em que estão inseridas é diferente e está relacionado a características intrínsecas de cada grupo (Wiens 1989).

Comparado com outros vertebrados, anuros possuem baixa capacidade de dispersão (Crnobrnja-Isailovic 2007, Qian 2009). Essa característica, associada ao fato de que anfíbios são altamente susceptíveis a mudanças em seus ambientes (Stuart *et al.* 2004), os tornam alvo para estudos de conservação (considerados bons indicadores de integridade e alteração ambiental) e modelos adequados para estudos ecológicos (Stebbins & Cohen 1995, Zug *et al.* 2001). A ordem Anura, táxon usado como modelo neste estudo, está representada por 6.458 espécies (Frost 2014), destas 988 espécies com distribuição no Brasil (Segalla *et al.* 2014), das quais mais de 250 ocorrem na Amazônia brasileira (Frost 2014). Além de alta riqueza de espécies, comunidades amazônicas possuem maior proporção de espécies em um único local de coleta quando comparadas com outras áreas de floresta tropical, como a Nova Guiné, e essa riqueza de espécies tende a crescer com o aumento da cobertura geográfica amostrada (Dahl *et al.* 2009). A distribuição de anuros amazônicos é altamente fragmentada quando comparada a outras comunidades de florestas tropicais, de forma que até mesmo locais geograficamente próximos possuem comunidades altamente dissimilares (Dahl *et al.* 2009).

Anuros apresentam alta diversidade reprodutiva, com aproximadamente 40 modos reprodutivos reconhecidos (e.g. Haddad & Prado 2005), e essas estratégias reprodutivas resultam de uma combinação de atributos morfológicos, fisiológicos e comportamentais (Duellman & Trueb 1986, Duellman 1989). Os modos reprodutivos das espécies estão diretamente associados às características do habitat em que os anuros vivem (Haddad & Prado 2005), e as condições ambientais de uma área podem restringir a diversidade local de modos reprodutivos dessas regiões (Duellman 1989, Hödl 1990, Bitar *et al.* 2012). Ou seja, cada tipo de ambiente exercerá pressões seletivas distintas sobre as espécies e seus modos reprodutivos, levando a um conjunto único de espécies especializadas às características ecológicas daquele local (Bitar *et al.* 2012). Por exemplo, espécies encontradas em áreas abertas tendem a se reproduzir na água ou em ninhos de espuma, diminuindo as chances de ressecamento dos ovos (Bitar *et al.* 2012). Por outro lado, espécies que se reproduzem na vegetação ou com desenvolvimento direto estão normalmente restritas a ambientes com alta umidade, tais como florestas de *terra firme* (Hödl 1990). Assim, esperamos que os diferentes ambientes encontrados na Amazônia, tais como terra firme, várzea, igapó e savanas, exerçam diferentes pressões seletivas sobre as espécies, sendo em parte selecionadas de acordo com seus modos reprodutivos.

Partindo do pressuposto acima, esperamos que os padrões estruturadores de uma comunidade de anuros estejam diretamente relacionados aos modos reprodutivos das espécies; espécies com diferentes modos reprodutivos devem responder de forma desigual aos fatores ecológicos influenciando a distribuição de cada grupo. Um exemplo disto foi encontrado por Landeiro *et al.* (2014), ao estudar comunidades de anuros no centro-oeste da Amazônia, onde o fator mais importante para o *turnover* das espécies com reprodução aquática foram as mudanças nas características ambientais, enquanto a variação na distância espacial foi mais importante para espécies terrestres. Isso acontece porque anuros com reprodução aquática necessitam de condições específicas para deposição de ovos e desenvolvimento dos girinos (e.g. distância da poça e densidade de árvores), enquanto as espécies com reprodução terrestre não têm sua distribuição restrita à presença de água, estando sua distribuição mais associada a sua habilidade de dispersão (Landeiro *et al.* 2014).

Além dos fatores ecológicos (espaço e ambiente), os resultados de um estudo sobre *turnover* também podem sofrer vieses metodológicos. Um desses fatores é a escala espacial utilizada. Estudos realizados em diferentes escalas podem obter resultados diferentes em relação ao *turnover* (Steinbauer *et al.* 2012). Por exemplo, fatores climáticos e históricos em geral, variam sobre a paisagem muito gradualmente, e, portanto, atuam como filtros em grandes escalas. Em contraste, muitos aspectos da estrutura do hábitat podem variar drasticamente em distâncias curtas, e portanto, atuam como filtros locais. Ao se considerar a escala de um estudo, tem que se ter em mente dois componentes muito importantes, o grão (tamanho da unidade amostral) e a extensão (área total considerada no estudo). Se o tamanho do grão é muito pequeno, o *turnover* será aumentado por fatores estocásticos e difícil de se relacionar com gradientes ecológicos (alta relação de ruído-sinal). Por outro lado, se o tamanho do grão é muito grande, então cada unidade amostral se torna internamente tão heterogênea que o *turnover* entre unidades amostrais se torna muito baixo (Tuomisto 2010b, Steinbauer *et al.* 2012, Barton *et al.* 2013). Já o aumento da extensão de um estudo, muitas vezes adiciona novos hábitats ou, pelo menos, estende os gradientes ambientais incluídos nas análises. Assim, a variação no grão e extensão estão fortemente correlacionados entre si e com a medição do *turnover* de espécies, devendo ser escolhidos de acordo com a percepção do ambiente pelo organismo modelo, de modo a refletir a sua biologia (Barton *et al.* 2013).

Assumindo que o ambiente e o espaço são elementos fundamentais na determinação do *turnover* entre as comunidades de anfíbios anuros; que a escala de observação pode influenciar na percepção dos resultados; e que, além disso, as espécies apresentam atributos que são selecionados por fatores ecológicos distintos, estruturamos esta tese de modo a responder as seguintes perguntas. Quais os efeitos da degradação ambiental sobre o *turnover* de anuros em florestas de transição Amazônia-Cerrado? Quais fatores são os estruturadores do *turnover* em escalas locais e regionais para anuros de áreas bem preservadas em florestas de terra firme amazônicas? Finalmente, qual a importância do modo reprodutivo de cada comunidade para o *turnover* em áreas com fitofisionomias semelhantes? E entre tipos de hábitat distintos (terra-firme x várzea). Assim, foi possível avaliar como mudanças ocorridas (variações ambientais) tanto em ambientes preservados, quanto em ambientes impactados afetam o *turnover* nas comunidades de anfíbios.

O primeiro capítulo encontra-se publicado no *Journal of Herpetology* com o título de “**Anuran beta diversity in a mosaic anthropogenic landscape in**

transitional Amazon". O objetivo deste artigo foi identificar qual o efeito da degradação ambiental sobre o *turnover* de espécies; o segundo capítulo encontra-se submetido para publicação na revista *Biotropica* sob o título de "**Species turnover in Amazonian frogs: Low predictability and large differences among terra firme forests".** Neste artigo particionamos o *turnover* em espaço e ambiente de forma a testar se florestas de terra firme apresentam padrões similares de *turnover*; o terceiro e último capítulo, com o título de "**How differences in anuran reproductive modes can affect their turnover: comparing scales and habitats**", aborda a importância dos modos reprodutivos dos anuros sobre os padrões de *turnover* observados em florestas de várzea e terra firme na Amazônia.

REFERÊNCIAS BIBLIOGRÁFICAS

Alford, R.A., & Richards, S.J. 1999. Global Amphibian Declines: A Problem in Applied Ecology. *Annual Review of Ecology and Systematics* 30:133-165.

Barton, P.S., Cunningha, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Didham, R.K. 2013. The spatial scaling of beta diversity. *Global Ecology and Biogeography* 22: 639–647.

Beebee, T.J.C. 1996. Ecology and Conservation of Amphibians. Chapman and Hall, United Kingdom.

Bielby, J., Cooper, N., Cunningham, A.A., Garner, T.W.J. & Purvis, A. 2008. Predicting susceptibility to rapid declines in the world's frogs. *Conservation Letters* 1:82-90.

Bitar, Y.O.C., Pinheiro, L.P.C., Abe, P.S., and Santos-Costa, M.C. 2012. Species composition and reproductive modes of anurans from a transitional Amazonian forest, Brazil. *Zoologia* 29:19-26.

Bitar, Y. O. C., L. Juen, L. P. C. Pinheiro and M. C. Santos-Costa. 2015. Anuran Beta Diversity in a Mosaic Anthropogenic Landscape in Transitional Amazon. J. Herpetol. In-Press.

Conte, C.E., & Machado, R.A. 2005. Riqueza de espécies e distribuição espacial e temporal em comunidade de anuros (Amphibia, Anura) em uma localidade de Tijucas do Sul, Paraná, Brasil. *Revista Brasileira de Zoologia* 22:940-948.

Crnobrnja-Isailovic, J. 2007. Cross-section of a refugium genetic diversity of amphibian and reptile populations in the Balkans. In: Weiss, S. Ferrand, N. (eds). *Phylogeography of southern European refugia*. Netherlands: Springer. 327–337.

Dahl, C., Novotny, V., Moravec, J. & Richards, S.J. 2009. Beta diversity of frogs in the forests of New Guinea, Amazonia and Europe: contrasting tropical and temperate communities. *Journal of Biogeography* 36:896–904.

Duellman, W.E. 1989. Alternative life-history styles in anuran amphibians: evolutionary and ecological implications. In: Bruton, M.N (Ed.), *Alternative life-history styles of animals.* Kluwer Academic Publishers, Dordrecht, p.101-126.

Duellman, W.E. & Trueb, L. 1986. *Biology of amphibians*. McGraw-Hill, New York.

Fonseca, A., Souza Jr., C., & Veríssimo, A. 2014. Boletim do desmatamento da Amazônia Legal (dezembro de 2014) SAD (p. 9). Belém: Imazon.

Frost, D.R. 2014. Amphibian Species of the World: an Online Reference. Version 6.0 (January 2015). Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

Gaston, K.J. & Chown, S.L. 2005. Neutrality and the niche. *Functional Ecology*, 19:1-6.

Grinnell, J. 1917. The niche-relationship of the California thrasher. *Auk* 34:427–33.

Haddad, C.F.B. & Prado, C.P.A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil. *BioScience* 55(3):207-217.

Hazell, D., Cunningham, D.L., Mackey, B., & Osborne, W. 2001. Use of farm dams as frog habitat in an Australian agricultural landscape: factors affecting species richness and distribution. *Biological Conservation* 102:155-169.

Hödl, W. 1990. Reproductive diversity in amazonian lowland frogs. *Fortschritte der Zoologie* 38:41-60.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H. & Kuzmin, S.L. 2000. Quantitative evidence for global amphibian population declines. *Nature* 404:752-755.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, New Jersey.

Hutchinson, M.F. 1957 Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22:415–427.

Landeiro, V.L., Waldez, F. & Menin, M. 2014. Spatial and environmental patterns of Amazonian anurans: Differences between assemblages with aquatic and terrestrial reproduction. *Natureza e Conservação* 12(1):42-46.

McGill, B.J., Maurer, B.A. & Weiser, M.D. 2006. Empirical evaluation of neutral theory. *Ecology* 87: 1411–1423.

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A.I., Basset, Y., Janda, M., Setliff, G.P., Darrow, K., Stewart, A.J.A., Auga, J., Isua, B., Molem, K., Manunbor, M., Tamtiai, E., Mogia, M. & Weiblen, G.D. 2007. Low beta diversity of herbivorous insects in tropical forests. *Nature* 448: 692–695.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., & Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19:18-24.

Qian, H. 2009. Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. Journal of Systematics and Evolution 47: 509–514.

Qian, H. and R. E. Ricklefs. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography* 21: 341–351.

Segalla, M.V., Caramaschi, U., Cruz, C.A.G., Grant, T., Haddad, C.F.B., Langone, J.A., & Garcia, P.C.A. 2014. Brazilian Amphibians: List of Species. *Herpetologia Brasileira*, 3 (2): 37-48.

Soininen, J., McDonald, R. & Hillebrand, H. 2007. The distance decay of similarity in ecological communities. *Ecography* 30: 3-12.

Stebbins, R.C., & Cohen, N.W. 1995. *A Natural History of Amphibians*. Princeton University Press, USA.

Steinbauer, M., Dolos, K., Reineking, B. & Beierkuhnlein, C. 2012. Current measures for distance decay in similarity of species composition are influenced by study extent and grain size. *Global Ecology and Biogeography* 21, 1203-1212.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller. R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783-1786.

Tuomisto, H. 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33: 2-22.

Tuomisto, H. 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33: 23-45.

Tuomisto, H. Ruokolainen, K. & Yli-Halla, M. 2003. Dispersal, environment and floristic variation of western amazonian forest. *Science* 299: 241-244.

Tuomisto, H., Zuquim, G. & Cárdenas, G. 2014. Species richness and diversity along edaphic and climatic gradients in Amazonia. *Ecography* 37:1034-1046.

Vasconcelos, T.S. & Rossa-Feres, D.C. 2005. Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do Estado de São Paulo, Brasil. *Biota Neotropica* 5:1-14.

Von May, R., J. M. Jacobs, R. Santa Cruz, J. Valdivia, J. Huamán, and M. A. Donnelly. 2010. Amphibian community structure as a function of forest type in Amazonian Peru. *Journal of Tropical Ecology* 26: 509-519.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecologycal Monographs* 30(3): 279–338.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology*, 3:385–397.

Zug, G.R., Vitt, L.J. & Caldwell, J.P. 2001. *Herpetology: an introductory biology of amphibians and reptiles*. Academic Press, USA

Zuquim, G., Hanna, T., Costa, F.R.C., Jefferson, P., Magnusson, W.E., Pimentel, T., Braga-Neto, R. & Figueiredo, F.O.G. 2012. Broad Scale Distribution of Ferns and Lycophytes along Environmental Gradients in Central and Northern Amazonia, Brazil. *Biotropica* 44: 752-762.

Capítulo 1

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Anuran beta diversity In A Mosaic Anthropogenic Landscape In Transitional Amazon

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Anuran beta diversity In A Mosaic Anthropogenic Landscape In Transitional Amazon

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RRH: Anuran beta diversity in disturbed forests

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Abstract.— Can the loss of forest habitat cause changes in local communities? The results of our study of anuran assemblages in the southern Amazon indicate that the conversion of forest into open environments results in the substitution of species and the reduction of beta diversity. The increasing loss of tropical forests to agricultural development, especially in the Amazon, has resulted in the extensive modification of the natural landscape, transforming once-continuous forests into a mosaic of modified habitats. Our data indicate that this process resulted in the substitution of forest species by generalists, which are more typical of open environments. Also, this process has a homogenizing effect, making different areas more similar to one another, resulting in a decrease in beta diversity. This substitution–homogenization process may become increasingly common through the ongoing advance of agricultural frontiers, resulting in the local extinction of an important component of the biodiversity of tropical forests.

Key words: Amazonia; Faunal homogenization; Habitat disturbance; Species loss; Species substitution; Transitional forest.

One of the fundamental questions in ecology is the understanding of the spatial and temporal distribution of species and the factors that determine this distribution (Angermeier and Winston, 1998). The diversity of a given area may be measured in a number of different ways, but the most commonly used indices are based on the variation in species composition in relation to a spatial or temporal gradient. These indices may be divided into alpha (a) diversity, which refers to local species richness, beta (b) diversity, which refers to the dissimilarities between two or more sampling sites (among-site variation in communities), and gamma (c) diversity, which is the total species richness found within a region (Whittaker, 1972; Loreau, 2000).

Because β diversity consists basically of the difference in the species composition of a community along an environmental gradient (Whittaker, 1972) or between habitats (Magurran, 1988; Jost, 2006, 2007), geographic distance and variations in the environmental characteristics of different sample areas are important determining factors. In this case, β diversity is determined by the response of species to variation among sites and reflects the degree of habitat specialization of the different species (Shmida and Wilson, 1985; Jankowski *et al.*, 2009; Melo *et al.*, 2009). Landscape-level characteristics, such as complexity and heterogeneity, have a major influence on β diversity, and an increase in both of these variables tends to provoke an increase in species diversity (Mac Arthur *et al.*, 1962; Levins, 1968). Complex habitats tend to have more and better developed vertical strata (August, 1983), whereas simpler habitats are less well developed. Heterogeneity refers to the horizontal variation in the landscape, with ample variation in the vegetation corresponding to high heterogeneity (August, 1983). In this case, environments with a mosaic of habitats with distinct vegetation characteristics will tend to have high β diversity, given that they will normally support communities with different ecological requirements.

The potential effects of changes in the landscape on the characteristics of local communities have received ample attention in the recent literature (e.g., Knutson *et al.*, 1999; Herrmann *et al.*, 2005; Soares Filho *et al.*, 2006). Modifications of the environment may have a homogenizing effect, reducing the complexity of habitats and, in turn, species richness (Hazell *et al.*, 2001; Olden *et al.*, 2004; Conte and Machado, 2005; Vasconcelos and Rossa-Feres, 2005). The increasing conversion of forest habitats into anthropogenic landscapes observed over the past few decades is one of the principal factors determining the decline and extinction of species throughout the world and, thus, of the loss of biodiversity in general (Beebee, 1996; Alford and Richards, 1999). Also, the loss of natural habitats is increasing in the Amazon (Fearnside, 2006), which is made up of an enormous variety of habitats and ecological conditions and is one of the most biologically diverse regions in the world (Gentry, 1988; Tuomisto *et al.*, 1995; Tuomisto and Ruokolainen, 1997). The original, continuous forests of this biome are being converted into a mosaic of isolated fragments and modified habitats, with significant impacts on both landscapes and ecological processes (Silva *et al.*, 2005; Hayhoe *et al.*, 2011).

The capacity of the fauna to respond to these changes in the landscape is still poorly understood, although the distribution and diversity of species is associated directly with ecological factors and the quality and distribution of habitats (Tuomisto and Ruokolainen, 1997). We used anuran assemblages as a predictive model system for the evaluation of the effects of the conversion of continuous forest into open areas for agriculture on β diversity. The anurans are one of the most diverse vertebrate groups in the world (Frost, 2011) and provide an excellent model for the investigation of the relationship between species and the environment, given their sensitivity to variations in factors, such as precipitation (Sinsch, 1990), humidity (Vonesh, 2001; Haddad and Prado, 2005), altitude (Fauth *et al.*, 1989), pollution (Stuart *et al.*, 2004), habitat quality (Crump, 1971; Gascon, 1991; Ernst and Rödel, 2008), and the presence of water bodies (Zimmerman and Bierregaard, 1986). Also, Anurans tend to have limited dispersal potential (Sinsch, 1990), and although most species depend on aquatic habitats for reproduction, they are also dependent on terrestrial habitats for foraging and migrating (Stebbins and Cohen, 1995; Zug *et al.*, 2001). In addition, natural or anthropogenic stressors in these habitats may directly influence amphibian's population (Salice *et al.*, 2011).

The conversion of forests into more open habitats tends to reduce the availability of habitats for anurans, in particular breeding sites, and generally results in an increase in the relative abundance of species adapted to open areas (Aichinger, 1991; Alves *et al.*, 1999; Tapia-Coral *et al.*, 1999; Vitt and Caldwell, 2001). In general, open areas are less favorable to species adapted for forested habitats (Becker *et al.*, 2007; Bernarde and Macedo, 2008), given their more specific ecophysiological requirements to microclimate conditions, especially on systems with high humidity such as in the Amazon rainforest. These forest species tend to play an important role in the conservation of local diversity and are normally responsible for relatively high levels of β diversity.

Given these considerations, we tested whether 1) degraded environments tend to be more similar because of the homogenization of habitats, whereas gallery forests present a higher turnover of species attributable to the greater availability of microhabitats, reflecting the generally higher β diversity in these environments; and 2) there is any difference in species composition in the habitats sampled, assuming that species with an Amazonian distribution are found in forested environments attributable to their greater dependence on more humid habitats and the presence of permanent water bodies, whereas species of the Cerrado savannas are better adapted to drier environments with temporary ponds and, thus, are able to persist in more affected habitats.

MATERIAL AND METHODS

Study Area.— The study area is located on the Fazenda Tanguro (Figure 1), a ranch in the municipality of Querencia, in the Brazilian state of Mato Grosso (datum SAD 69, 13'04035.3900 S, 52'23008.8500 W), within a transition zone between the Amazonian forest and Cerrado savanna biomes, which is vulnerable to the ongoing expansion of agricultural frontiers in the region known as the ''Arc of deforestation'' (Balch *et al.*, 2008; Hayhoe *et al.*, 2011; Bitar *et al.*, 2012). This property encompasses an area of 82,000 ha, of which 38,000 ha are agricultural land (soybean and rubber plantations) and 44,000 ha are forest, natural gallery forest, or regenerating habitat. The climate of the region is humid tropical with a marked dry season, of the Aw type (Peel *et al.*, 2007), with mean annual precipitation of 1,900 mm and mean annual temperature of 278C (Hayhoe *et al.*, 2011).

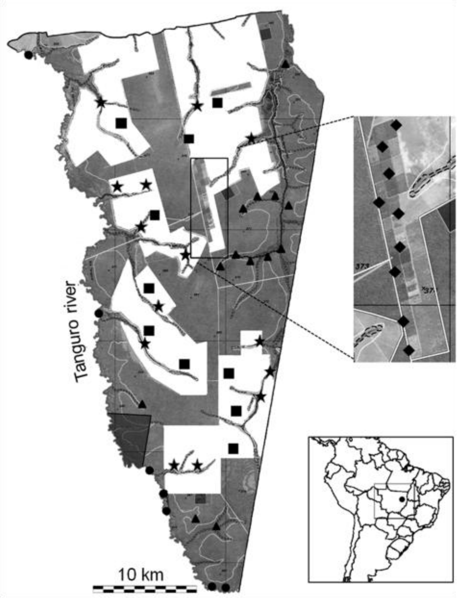

FIG. 1. Location of sample plots at the Fazenda Tanguro, Querência, Mato Grosso (Brazil). In the larger map, white areas correspond to agricultural land, whereas gray areas represent the forest. Plots are distinguished by habitat type: squares = deforested area (DEF); circles = margin of the Tanguro River (TAN); diamonds = rubber plantation (RUB); triangles = preserved gallery forest (PGF); stars = disturbed gallery forest (DGF). Modified from Balch *et al.* (2008).

Characterization of Habitats.— Five different habitat types were sampled: preserved gallery forest (PGF), disturbed gallery forest (DGF), margin of the Tanguro River (TAN), rubber plantation (RUB), and deforested areas (DEF).

Gallery forests consist of arboreal vegetation that grows alongside water bodies, which may vary considerably in width and species composition (Ab'Sáber, 2001). Plots were classified as preserved gallery forest when they were located at least 850 m from the nearest deforested area and as disturbed gallery forest when they were located no more than 35 m from a deforested area. In both cases, the water bodies are perennial streams and creeks with margins that flood during the rainy season.

The Tanguro River (width greater than 10 m) is lotic and has well-defined margins with marked depressions that allow lentic areas attributable to either the high water table or the accumulation of water during the rainy season. This type of habitat can be considered a type of gallery forest (Ab'Sáber, 2001), although we allocated it to a different category (TAN) because of the presence of distinct characteristics.

In the rubber plantations, rubber trees (*Hevea brasiliensis*) are arranged in a regular pattern, with no undergrowth between them. In these areas, the only water bodies are temporary pools that form following heavy rain. The deforested areas are used for planting annual crops and are made up of open fields with exposed soil and no vegetation or leaf litter, with drainage ditches in which rainwater accumulates but with no marginal vegetation.

Experimental Design.— Fifty-four sample plots were established to provide a reliable sample of the heterogeneity of habitats found within the study area. Using satellite imagery, the plots were distributed according to the availability of water bodies and at least 500 m from the nearest plot on the five different habitat types identified during the initial survey (see above) to minimize the effect of spatial autocorrelation of environmental characteristics (Legendre, 1993). All plots contained at least one water body to equalize biases related to water availability and the richness of water-dependent species. Plots were arranged within the different habitat types according to the distribution of water: 13 plots were located in preserved gallery forest, 15 in disturbed gallery forest (surrounded by open fields prepared for crops), 7 on the margins of the Tanguro River, 9 in the rubber plantations, and 10 in the deforested area (Fig. 1). Ninety days of field excursions, divided in two 45-day field expeditions, were conducted during the 2008–2009 rainy season, one between 21 October and 7 December 2008, and the second between16 February and 4 April 2009.

Each sampling unit corresponded to a 100 x 50 m plot (0.5 ha) separated by a distance of at least 500 m from the nearest plot, within which active and auditory searches were conducted on one occasion in each plot (Zimmerman, 1994; Crump and Scott 1994) between 2000 h and 2400 h. Plots were surrounded by a string, demarcating its boundaries, and inside the plots, surveys were performed using standardized sampling methods: visual sampling (visual encounter surveys) and auditory survey, simultaneously (Crump and Scott 1994, Zimmerman 1994, Menin *et al.* 2007). Each plot was covered by three people walking side by side for at least 2 h or until no new specimens were recorded. Approximately every 5 m, the observers stopped and registered the number of individuals of each species that were calling. At the same time, they searched visually in the leaf litter and in the surrounding vegetation. All frog sightings and all calls heard inside the plot were counted.

Environmental Variables.—Four variables, were measured in each plot: number of trees, circumference at breast height (CBH), litter height, and canopy cover. Litter height (cm): Four equidistant dry points were chosen systematically to measure the height of the litter and the average value representing the plot. We determined the value using methods developed by B. H. Marimon Jr. and J. D. Hay (Patent PI – 0505830-9/ UNB/UNEMAT). Canopy cover (%): We used the average of four photos per plot taken with a digital camera attached to a spherical lens and the use of a tripod with the camera at 50 cm above the ground. CBH (cm) and number of trees: Two smaller parcels of 10 · 5m were chosen at random inside each plot, and each liana or tree with CBH > 5 cm was measured. The value of the sum of the two smaller parcels was recorded and was representative of that plot.

Statistical Analysis. —Because the species richness recorded (observed) at a given site is frequently an underestimate of the true number of species at that site (Santos, 2003), a first-order nonparametric Jackknife estimator (Heltshe and Forrester, 1983; Coddington *et al.*, 1991; Colwell and Coddington, 1994) was used based in 1,000 interactions to estimate the number of species within the study area and in each of the five habitats sampled. This approach provides a more reliable estimate of the number of species present in a community (Krebs, 1999) and also a confidence interval, which allows systematic statistical comparisons between the values estimated for two or more sites.

The variation in the composition of species among plots (β diversity) was estimated for each sample using Sorensen’s quantitative index with the modification of Chao *et al.* (2005). This index was chosen because it takes not only species abundance into consideration but also an estimate of the species that may not have been identified in the sample. Also, it is considered to be relatively independent of species richness, and more accurate, even for small samples (Soininen *et al.*, 2007). The Sorensen index was calculated for all pairs of plots. Higher values correspond to a more differentiated species composition. The mean Sorensen index, calculated for the whole set of plots, was used as an estimator of β diversity for each type of habitat. Differences in abundance and β diversity among the habitat types were evaluated using a one-way analysis of variance, or ANOVA (Zar, 1999). The assumptions of normality and homoscedasticity were assessed using Levene's test. When significant differences were found, Tukey's a posteriori test was applied to identify the habitats, which were significantly different from one another. A Principal Coordinates Analysis, or PCoA (Anderson and Willis, 2003), was used to summarize the data on the structure and composition of the anuran assemblage, as well as to verify which species contributed most to the ranking of the habitats. This analysis was based on both quantitative (absolute abundance on each plot) and qualitative (presence/absence) data. Sorensen's index was used as a measure of distance for the analysis of the quantitative data (Chao *et al.*, 2005), whereas the qualitative data were analyzed using Jaccard's distance. An Analysis of Similarity (ANOSIM) was used to evaluate the differences in the species composition in the PCoA ranking. To access the contribution of the species to each PCoA axes, a correlation were made between matrices (quantitative and qualitative) and the first and second axes of the PCoA.

The relative species contribution to β diversity (SCBD) was determined based on the partition of total β diversity proposed by Legendre and De Cáceres (2013), using the Hellinger distance. Habitat heterogeneity was calculated using the distance-based test for homogeneity of multivariate dispersion (Anderson, 2006) on the environmental data of each habitat, using the Euclidian distance. To test whether the habitats were different according to the environmental variables, we used a ANOSIM with Euclidian distance on these variables. All statistical analyses were conducted with the statistical software R version 2.15.1 (R Development Core Team; http:// www. R-project.org).

RESULTS

Seven hundred thirty-nine specimens were collected, representing 26 species belonging to six families. Fifteen species were recorded in the disturbed gallery forest (DGF), whereas in the preserved gallery forest (PGF), 10 species were recorded (Table 1). The estimated species richness was very similar for the two types of habitat, and approximately 1.65 times higher than the value recorded in more degraded habitats (RUB and DEF). Based on the confidence intervals, the difference between DGF and PDF was not significant. The plots on the margins of the Tanguro River (TAN) were the least species rich. On average, the gallery forests (PGF and DGF) and anthropogenic (RUB and DEF) habitats had 2.32 and 1.41 more species, respectively, than did TAN (Fig. 2A).

TABLE 1. Abundance (number of specimens) of the different anuran species recorded in the five different habitat types surveyed on the Fazenda Tanguro in Mato Grosso, Brazil. DGF = disturbed gallery forest; PGF = preserved gallery forest; TAN = margin of the Tanguro River; RUB = rubber plantation; DEF = deforested area.

	DGF	PGF	TAN	RUB	DEF	Total abundance
BUFONIDAE						
Rhinella mirandaribeiroi (Gallardo, 1965)	0	0	0	0	6	6
Rhinella schneideri (Werner, 1894)	0	1	0	3	0	4
HYLIDAE						
Dendropsophus melanargyreus (Cope, 1887)	0	0	0	2	3	5
Dendropsophus minutus (Peters, 1872)	0	0	0	13	0	13
Dendropsophus nanus (Boulenger, 1889)	32	6	0	0	0	38
Hypsiboas albopunctatus (Spix, 1824)	38	30	0	0	0	68
Hypsiboas boans (Linnaeus, 1758)	0	0	1	0	0	1
Hypsiboas cinerascens (Spix, 1824)	56	89	11	0	0	156
Hypsiboas geographicus (Spix, 1824)	0	0	13	0	0	13

Osteocephalus cf. *taurinus* Steindachner, 1862	103	53	0	0	0	156
Osteocephalus sp.	16	16	0	0	0	32
Scinax fuscomarginatus (A. Lutz, 1925)	15	0	0	0	0	15
Scinax fuscovarius (A. Lutz, 1925)	1	0	0	9	6	16
Scinax nebulosus (Spix, 1824)	6	0	0	0	0	6
LEIUPERIDAE						
Eupemphix nattereri Steindachner, 1863	2	0	0	0	15	17
Physalaemus centralis Bokermann, 1962	1	0	0	0	5	6
Physalaemus cuvieri Fitzinger, 1826	7	0	0	0	2	9
LEPTODACTYLIDAE						
Leptodactylus fuscus (Schneider, 1799)	0	0	0	52	49	101

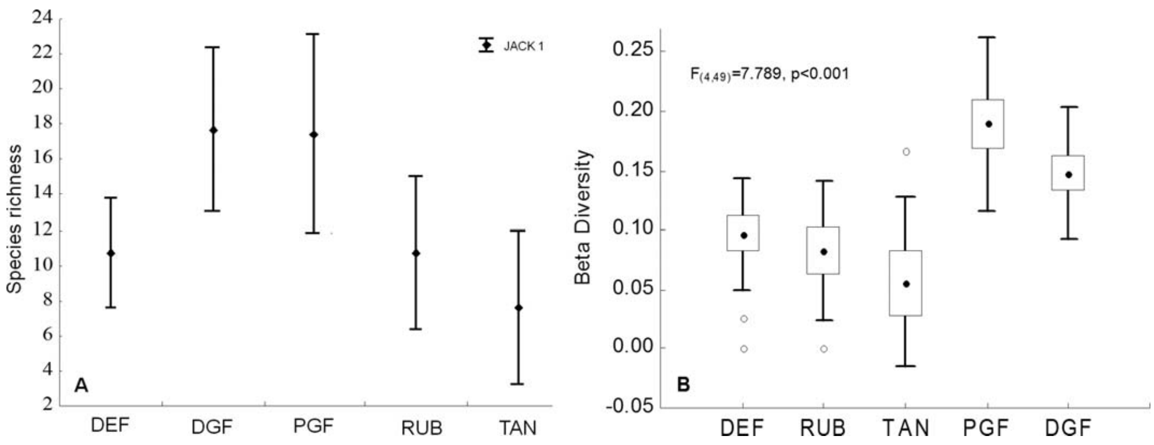

FIG. 2. (A) Estimated species richness of aurans in each habitat type (vertical bars represent the 95% confidence interval); (B) mean β diversity (dots = mean; bars = ± SE; lines = ± SD; open circles = outliers) recorded in each habitat type. DEF = deforested area; DGF = disturbed gallery forest; PGF = preserved gallery forest; RUB = rubber plantation; TAN = margin of the Tanguro River.

The first two axes of the PCoA for the quantitative data (abundance) captured a total of 55.41% of the variation in the data (axis 1 = 39.51%, axis 2 = 15.90%), revealing three distinct groupings (ANOSIM, P < 0.01, Global R = 0.4788). The first group includes both types of gallery forest (Fig. 3A), the second group, the deforested areas and rubber plantations, and the third, the margins of the Tanguro River, which is clearly distinct from all the other types of habitat. However, when we considered the qualitative (presence/absence) data (Fig. 3B), the first two axes of the PCoA captured only 36.59% of the variation observed in the data (axis 1 = 25.89%, axis 2 = 10.70%), and in this case, the deforested areas and rubber plantations were also distinguished significantly (ANOSIM, $P < 0.01$, Global $R = 0.4869$). According to the partition of β diversity (Legendre and De Cáceres 2013), the species that contributed more were *L. fuscus, H. cinerascens* and *O. taurinus*, respectively (Fig. 3), a similar pattern to that observed when the PCoA axes were correlated with the quantitative and qualitative matrices (Fig. 3A,B).

In the rubber plantations and deforested areas, which are highly degraded areas with temporary pools, the predominant species were those typical of the Cerrado: *Eupemphix nattereri, Physalaemus centralis, Rhinella schneideri,* and *Scinax fuscovarius*. Three species (*Dendropsophus melanargyreus, Elachistocleis ovalis,* and *Leptodactylus fuscus*) were found exclusively in these habitats. Typically Amazonian species, such as *Osteocephalus* cf. *taurinus* and *Hypsiboas cinerascens* (each represented by 156 specimens), predominated in the forested habitats (PGF, DGF, and TAN), and 12 of these were exclusive to these habitats. In addition to *O*. cf. *taurinus*, nine species were found only in gallery forest: *Pristimantis fenestratus, Hypsiboas albopunctatus, Osteocephalus* sp., and *Leptodactylus paraensis.*

Using the environmental variables, we found no difference between DGF, PGF, and TAN, but DES and RUB were different from all other habitats (ANOSIM, $P < 0.01$, Global $R = 0.53$). Environmental heterogeneity was different among habitats ($F4,48 = 3.834$; $P = 0.012$). Heterogeneity were highest in habitats with natural vegetation (DGF, PGF, TAN) than in the rubber plantations and deforested areas, but this difference was only significant between DEF and the others ($P < 0.001$). Considering the environmental variables, DEF and RUB were different from all the other habitats and had no difference between forested areas (ANOSIM, $P < 0.001$, Global $R = 0.53$). Respectively, habitat heterogeneity (average distance to centroid) was higher in DGF (1.092), PGF (0.630), TAN (0.571), RUB (0.456), and DEF (< 0.001).

Beta diversity was significantly different among habitats ($F_{4,49} = 7.789$, $P < 0.001$). The two gallery forest categories (PGF and DGF) were the habitats with the highest β diversity (Fig. 2B). Although diversity was 0.042 higher, on average, in PGF in comparison with DGF, this difference was not significant (Tukey's test, $P = 0.394$). Mean β diversity in the rubber plantations ($P = 0.002$) and deforested areas ($P = 0.007$) was approximately half that recorded in the preserved gallery forest, whereas that recorded on the margin of the Tanguro River (TAN) was even lower ($P < 0.001$). The only significant difference found between disturbed habitats was that between DGF and TAN ($P < 0.017$).

The first two axes of the PCoA for the quantitative data (abundance) captured a total of 55.41% of the variation in the data (axis 1 = 39.51%, axis 2 = 15.90%), revealing three distinct groupings (ANOSIM, $P < 0.01$, Global $R = 0.4788$). The first group includes both types of gallery forest (Fig. 3A), the second group, the deforested areas and rubber plantations, and the third, the margins of the Tanguro River, which is clearly distinct from all the other types of habitat. However, when we considered the qualitative (presence/absence) data (Fig. 3B), the first two axes of the PCoA captured only 36.59% of the variation observed in the data (axis 1 = 25.89%, axis 2 = 10.70%), and in this case, the deforested areas and rubber plantations were also distinguished significantly (ANOSIM, $P < 0.01$, Global $R = 0.4869$). According to the partition of β diversity (Legendre and De Cáceres 2013), the species that contributed more were L. fuscus, H. cinerascens and O. taurinus, respectively (Fig. 3), a similar pattern to that observed when the PCoA axes were correlated with the quantitative and qualitative matrices (Fig. 3A,B).

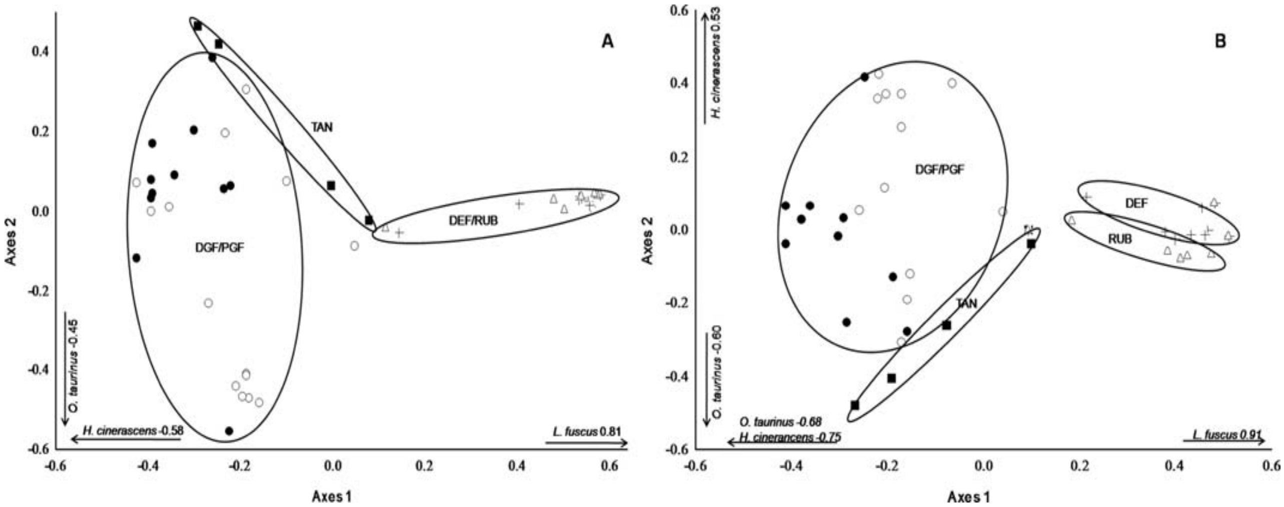

FIG. 3. Principal Coordinates Analysis (PCoA) with groups based on the Analysis of Similarity (ANOSIM) of the (A) quantitative data and (B) qualitative data on species composition. DGF = disturbed gallery forest (open circles); PGF = preserved gallery forest (black circles); RUB = rubber plantation (triangles); DEF = deforested area (crosses); TAN = margin of the Tanguro River (squares). Species over the arrows and their values represent the correlation of the species with each axis.

DISCUSSION

Our results indicate clearly that the suppression of forested areas or the substitution of the forest cover with plantations may alter both the species composition of an area and the dissimilarity among habitats (β diversity). Our data confirm the assumption that more complex habitats, with intermediate levels of disturbance, tend to have higher species richness (Grime, 1973; Horn, 1975; Connel, 1978; Souza, 1984; Rosenzweig, 1995; Tokeshi, 1999). However, even for these less affected areas, there may be a homogenization of the fauna through the insertion of generalist species with a greater dispersal capacity (Shmida and Wilson, 1985; Olden *et al.*, 2004; Marinoni and Ganho, 2006; Olden and Rooney, 2006), leading to a loss of β diversity.

The distribution of the species adapted to more open woodland habitats may also increase in the wake of deforestation and habitat disturbance (Haddad, 1998). These species, along with the generalists, in particular those with greater dispersal capacity, are much less susceptible to modifications of the environment (Diamond and May, 1976; Lovejoy *et al.*, 1984, 1986; Soulé, 1990; Haddad, 1998; Morato and Campos, 2000; Leandro and D'Almeida, 2005). In anthropogenic environments, the predominance of these species generally results in the homogenization of the biota, and reduced levels of β diversity (Olden *et al.*, 2004; Soininen *et al.*, 2007).

The mosaic of habitats that results from anthropogenic impacts provoked significant modifications in the species composition of different areas, with the full or partial substitution of forest species by savanna species in degraded habitats (RUB and DEF). Because the remnant areas of forest represent the natural cover of the region prior to anthropogenic impact, the species encountered in these areas can be considered to be typical of the region's native fauna, whereas those found exclusively in the more degraded habitats can be classified as more opportunistic, invasive species. As observed in the Atlantic Forest and Cerrado (Brasileiro *et al.*, 2005; Moraes *et al.*, 2007), it seems likely that the ongoing advance of agricultural frontiers into the Amazon biome, and the substitution of the original forest by more open, anthropogenic habitats, will lead to the substitution of typically Amazonian species by others normally found in the Cerrado, which are more tolerant to disturbance and better adapted to hydrological stress and high temperatures.

Beta diversity is often related closely to environmental heterogeneity (Whittaker, 1972; Legendre *et al.*, 2005), and habitats with a greater heterogeneity tend to favor higher values of β diversity, but this relationship is not always positive (e.g., Ralph, 1985; Sullivan and Sullivan, 2001; Tews *et al.*, 2004; González-Megias *et al.*, 2007; Jay-Robert *et al.*, 2008). Nevertheless, studies of groups that are well adapted to forested habitats and are relatively diverse in the tropics, such as amphibians (e.g. Atauri and Lucio, 2001), birds (e.g. Wiens and Rotenberry, 1981; Thiollay, 1990; Poulsen, 2002), mammals (e.g., August, 1983; Dueser and Porter, 1986; Southwell *et al.*, 1999; Williams *et al.*, 2002), and arthropods (e.g., Haslett, 1997; Brose, 2003; Lassau and Hochuli, 2004), have all shown that diversity tends to be greater in more heterogeneous environments (see Lassau and Hochuli, 2004; Tews *et al.*, 2004). We suggest that the greater dissimilarity found in the fauna of the gallery forests may be related directly to the capacity of these environments to support more species, because of the availability of distinct microhabitats.

The distribution of anurans tends to be related closely to the distribution of water bodies, especially during the breeding season (Bernarde, 2007). In the gallery forests, these environments are perennial and are naturally impounded in many locations, providing breeding sites for species that reproduce in both lotic and lentic environments (Bitar *et al.*, 2012). Also, forest habitats are much less susceptible to sudden changes in temperature and humidity, which makes these habitats more stable and, thus, more favorable to a larger number of species than areas of secondary habitat, which may be more variable to temperature and humidity fluctuations and also be at a successional stage characterized by the recolonization of native species and the colonization of invasive species (Scott, 1982; Heinen, 1992).

The characteristics of the vegetation found within a given area reflect its history of disturbance systematically and determine the differences in diversity and species composition found between pristine and disturbed habitats (Iger and Colwell, 1977;

Heinen, 1992; Tocher, 1998). Changes in the patterns of dominance and relative abundance of species between primary and secondary forest have been shown in a number of anuran studies (Lieberman, 1986; Heinen, 1992; Tocher, 1998; Machado *et al.*, 1999; Ernst and Rödel, 2005). This may be related to three principal factors: 1) the capacity of some species to colonize disturbed habitats; 2) the physiological tolerance of species in relation to environmental conditions; and 3) the requirements of some species for specific microhabitats. Moraes *et al.* (2007) identified these factors in relation to anuran communities in the Brazilian Atlantic Forest, and they appear to be equally relevant to our results.

We recorded the lowest values of species richness and β diversity on the margins of the Tanguro River, within forested habitat. This apparent contradiction may be related to the reduced availability of microhabitats favorable to the reproduction of the species we recorded, which use mainly lentic and temporary water bodies as spawning sites. Some of the species, such as *Hypsiboas boans* and *Hypsiboas geographicus*, present reproductive modes that permit spawning in lotic environments, and these species predominate on the margins of the river and its tributaries, whereas species not well adapted to the relatively strong currents of these aquatic environments are not found in this area (Zimmerman and Bierregaard, 1986; Hödl, 1990).

We provide further evidence that the distribution of species typical of the Cerrado savanna is expanding into the areas of the Amazon that have suffered widespread anthropogenic impacts, resulting in the substitution of native species by those better adapted to more open conditions. This process may become increasingly common as agricultural frontiers expand leading to the local extinction of an important component of the biome’s diversity. Also, this process results in the homogenization of the fauna and the loss of β diversity, given the lack of substitutions within or between habitat types. Olden *et al.* (2004) consider homogenization to be one of the principal factors determining the loss of biodiversity worldwide, and although the understanding of the effects of this process on the biota of both aquatic and terrestrial ecosystems is growing, the long-term consequences are still obscure. Clearly, the substitution of species has a strong influence on diversity (Condit *et al.*, 2002), and the systematic understanding of the distribution of species along a given environmental gradient may represent an extremely important resource for the planning of effective conservation strategies (Carvalho, 2006).

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LITERATURE CITED

Ab'Sáber, A.N. 2001. O suporte geológico das florestas beiradeiras (ciliares). Pp. 15-25 in Rodrigues, R.R. and Leitão Filho, H.F. (Eds.), Matas ciliares: conservação e recuperação. Edusp, Brasil

Aichinger, M. 1991. Faunal deficit of anurans in tropical farmland of Amazonian Peru. Alytes 9:23-32

Alford, R.A., and Richards, S.J. 1999. Global Amphibian Declines: A Problem in Applied Ecology. Annual Review of Ecology and Systematics 30:133-165

Alves, F.S.M., Fisch, G., and Vendrame, I.F. 1999. Modificações do microclima e regime hidrológico devido ao desmatamento na Amazônia: estudo de um caso em Rondônia (RO), Brasil. Acta Amazonica 29:395-409

Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245-253

Anderson, M.J., and Willis, T.J. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511-525

Angermeier, P.L., and Winston, M.R. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. Ecology 79:911-927

Atauri, J.A., and Lúcio, J.V. 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecology 16:147-159

August, P.V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64:1495-1507

Balch, J.K., Nepstad, D.C., Brando, P.M., Curran, L.M., Portela, O., Carvalho Jr., O., and Lefebvre, P., 2008. A Negative Fire Feedback in a Transitional Forest of Southeastern Amazonia. Global Change Biology 14:2276-2287

Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F., and Prado, P.I. 2007. Habitat split and the global decline of amphibians. Science 318:1775-1777

Beebee, T.J.C. 1996. Ecology and Conservation of Amphibians. Chapman and Hall, United Kingdom

Bernarde, O.S., and Macedo, L.C. 2008. Impacto do desmatamento e formação de pastagens sobre a anurofauna de serapilheira em Rondônia. Iheringia 98:454-459

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

Bitar, Y.O.C., Pinheiro, L.P.C., Abe, P.S., and Santos-Costa, M.C. 2012. Species composition and reproductive modes of anurans from a transitional Amazonian forest, Brazil. Zoologia 29:19-26

Brasileiro, C.A., Sawaya, R.J., Kiefer, M.C., and Martins, M. 2005. Amphibians of an open Cerrado fragment in southeastern Brazil. Biota Neotropica 5:1-17

Brose, U. 2003. Island biogeography of temporary wetland carabid beetle communities. Journal of Biogeography 30:879-888

Carvalho, C.J.B. 2006. Padrões de endemismos e a conservação da biodiversidade. Megadiversidade 5:77-86

Chao, A., Chazdon, R.L., Colwell, R.K., and Shen, T.J. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8:148-159

Coddington, J.A., Griswold, C.E., Silva Dávila, D., Peñaranda, E., and Larcher, S.F. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pp. 44-60 in E.C. Dudley (Eds.), The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology. Dioscorides Press, Oregon

Colwell, R.K., and Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 345:101-118

Condit, R., Pitman, N., Leigh Jr., G.E., Chave, J., Terborgh, J., Foster, B.R., Núnez, V.P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., and Hubbell, S.P. 2002. Beta-diversity in tropical trees. Science 295:666-669

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310

Conte, C.E., and Machado, R.A. 2005. Riqueza de espécies e distribuição espacial e temporal em comunidade de anuros (Amphibia, Anura) em uma localidade de Tijucas do Sul, Paraná, Brasil. Revista Brasileira de Zoologia 22:940-948

Crump, M.L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. Occasional Papers of the Museum of Natural History, University of Kansas 3:1-62

Crump, M.L., and Scott Junior, N.J. 1994. Visual encounter surveys. Pp. 84-92 in Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.A.C., and Foster, M.S. (Eds.), Measuring and monitoring biological diversity: standart methods for amphibians. Smithsonian Institution Press, USA

Diamond, J.M., and May, R.M. 1976. Island biogeography and the design of natural reserves. Pp. 163-186 in May, R.M. (Eds.), Theoretical ecology. Saunders, USA

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., and Robert Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609-628

Dueser, R.D. and Porter, J.H. 1986. Habitat use by insular small mammals: relative effects of competition and habitat structure. Ecology 67:195-201

Ernst, R., and Rödel, M.O. 2005. Anthropogenically induced changes of predictability in Tropical anuran assemblages. Ecology 86:3111-3118

Ernst, R., and Rödel, M.O. 2008. Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environmental effects in disturbed and undisturbed forests. Journal of Tropical Ecology 24:111-120

Fauth, J.E., Crother, B.I., and Slowinski, J.B. 1989. Elevational Patterns of Species Richness, Evenness, and Abundance of the Costa Rican Leaf-Litter Herpetofauna. Biotropica 21:178-185

Fearnside, P.N. 2006. Desmatamento na Amazônia: dinâmica, impactos e controle. Acta Amazonica 36:395-400

Frost, D.R. 2011. Amphibian Species of the World: an Online Reference. version 5.5. New York: American Museum of Natural History. Available from: <http://research.amnh.org/vz/herpetology/amphibia/>

Gascon, C. 1991. Population and community-level analyses of species occurrences of central Amazonian rainforest tadpoles. Ecology 72:1731-1746

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75:1-34

González-Megias, A., Gómes, J.G., and Sánchez-Piñero, F. 2007. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. Ecography 30:31-41

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344-347

Haddad, C.F.B. 1998. Biodiversidade dos anfíbios no Estado de São Paulo. Pp. 17-26 in Castro, R.M.C. (Ed.), Biodiversidade do Estado de São Paulo, Brasil: síntese do conhecimento ao final do século XX. Editora Fapesp, Brazil

Haddad, C.F.B., and Prado, C.P.A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil. BioScience 55:207-217

Haslett, J.R. 1997. Mountain ecology: organism responses to environmental change, an introduction. Global Ecology and Biogeography Letters 6:3-6

Hayhoe, S.J., Neill, C., Porder, S., McHorney, R., LeFebvre, P., Coe, M.T., Elsenbeer, H., and Krusche, A.V. 2011. Conversion to soy on the Amazonian agricultural frontier increases streamflow without affecting stormflow dynamics. Global Change Biology 17:1821-1833

Hazell, D., Cunningham, D.L., Mackey, B., and Osborne, W. 2001. Use of farm dams as frog habitat in an Australian agricultural landscape: factors affecting species richness and distribution. Biological Conservation 102:155-169

Heinen, J.T. 1992. Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: some implications for faunal restoration. Biotropica 24:431-439

Heltshe, J.F., and Forrester, N.E. 1983. Estimating species richness using the JACKKNIFE procedure. Biometrics 39:1-11

Herrmann, H., Babbitt, K., Baber, M., and Gongalton R. 2005. Effects of landscape characteristics on amphibian distribution in a forest-dominated landscape. Biological Conservation 123:139-149

Hödl, W. 1990. Reproductive diversity in Amazonian lowland frogs. Fortschritte der Zoologie 38:41-60

Horn, H.S. 1975. Markovian properties of forest sucession. Pp.196-211 in Cody, M.L., and Diamond, J.M. (Eds.), Ecology and evolution of communities. Harvard University Press, United Kingdom

Inger, R.F., and Colwell, R.K. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. Ecological Monographs 47:229-253

Jankowski, J.E., Ciecka, A.L., Meyer, N.Y., and Rabenold, K.N. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. Journal of Animal Ecology 78:315-327

Jay-Robert, P., Errouissi, F. and Lumaret. J.P. 2008. Temporal coexistence of dung-dweller and soil-digger dung beetles (Coleoptera: Scarabaeidae) in contrasting Mediterranean habitats. Bulletin of Entomological Research 98:303-316

Jost, L. 2006. Entropy and diversity. Oikos 113:363-375

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427-2439

Knutson, M.G., Sauer, J.R., Olsen, D.A., Mossman, M.J., Hemesath, L.M., and Lannoo, M.J. 1999. Effects of landscape composition and wetland fragmentation on frog and toad density and species richness in Iowa and Wisconsin, USA. Conservation Biology 13:1437-1446

Krebs, C.J. 1999. Ecologycal methodology. Menlo Park, Addison Wesley Longman

Lassau, S.A., and Hochuli, D.F. 2004. Effects of habitat complexity on ant assemblages. Ecography 27:157-164

Leandro, M.J.F., and D'Almeida, J.M. 2005. Levantamento de Calliphoridae, Fanniidae, Muscidae e Sarcophagidae em um fragmento de mata na Ilha do Governador, Rio de Janeiro, Brasil. Iheringia, Série Zoologia 9:377-381

Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology 74(6):1659-1673

Legendre, P., Borcard, D., and Peres-Neto. P.R. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecologycal Monographs 75:435-450

Legendre, P., and De Cáceres, M. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology Letters 16: 951-963

Levins, R. 1968. Evolution in changing environments, some theoretical explorations. Princeton University Press, USA

Lieberman, S.S. 1986. Ecology of the leaf litter herpetofauna of a Neotropical rainforest: La Selva, Costa Rica. Acta Zoologica Mexicana 15:1-71

Loreau, M. 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. Ecology Letters 3:73-76

Lovejoy, T.E., Rankin, J. M.; Bierregaard, R. O.Jr.; Brown, K.S.Jr.; Emmons, L.H., and Van Der Voort, M.E. 1984. Ecosystem decay of Amazon forest remnants. Pp. 295-325 in Nitecki, M.H. (Ed.), Extinctions. University of Chicago Press, USA

Lovejoy, T.E., Bierregaard, R.O. Jr., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown Jr., K.S., Powell, A.H., Powell, G.V.N., Schubart, H.O.R., and Hays., M.B. 1986. Edge effects and other effects of isolation on Amazon forest fragments.Pp. 257-285 in Soulé , M.E. (Ed.), Conservation Biology: The

Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts

Mac Arthur, R.H., Mac Arthur, J.W., and Preer, J. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. The American Naturalist 99:167-174

Machado, R.A., Bernarde, P.S., Morato S.S.A., and Anjos, L. 1999. Análise comparada da riqueza de anuros entre duas áreas com diferentes estados de conservação no município de Londrina, Paraná, Brasil (Amphibia: Anura). Revista Brasileira de Zoologia 16:997-1004

Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Croom Helm, United Kingdom

Marinoni, R.C., and Ganho, N.G. 2006. A diversidade diferencial beta de Coleoptera (Insecta) em paisagem antropizada do Bioma Araucária. Revista Brasileira de Entomologia 50:64-71

Menin, M., Lima, A. P. Magnusson, W. E. and Waldez, F. 2007. Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns. Journal of Tropical Ecology 23:539–547

Melo, A.S., Rangel, T.F.L.V., and Diniz-Filho, J.A.F. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. Ecography 32:226-236

Moraes, R.A., Sawaya, R.J., and Barrella, W. 2007. Composição e diversidade de anfíbios anuros em dois ambientes de Mata Atlântica no Parque Estadual Carlos Botelho, São Paulo, sudeste do Brasil. Biota Neotropica 7:1-10

Morato, E.F., and Campos, L.A.O. 2000. Efeitos da fragmentação florestal sobre vespas e abelhas solitárias em uma área da Amazônia Central. Revista Brasileira de Zoologia 17(2):429-444.

Olden, J.D., and Rooney, T.P. 2006. On defining and quantifying biotic homogenization. Global Ecology and Biogeography 15:113-120

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., and Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19:18-24

Peel, M.C., Finlayson, B.L., and McMahon, T.A. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11:1633-1644

Poulsen, B.O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. Biological Conservation 11:1551-1566

Ralph, C.J. 1985. Habitat association patterns of forest and steppe birds of Northern Patagonia, Argentina. The Condor 87:471-483

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, United Kingdom

Salice, C.J., Rowe, C.L., Pechman, J.H.K., and Hopkins, W.A. 2011. Multiple stressors and complex life--cycles: Insights from a population--level assessment of breeding site contamination and terrestrial habitat loss in an amphibian. Environmental Toxicology and Chemistry 30: 2874-2882

Santos, A.J. 2003. Estimativas de riqueza em espécies. Pp.19-41 in Cullen Jr., L., R. Rudran, R., and C. Valladares-Pádua, C. (Eds.), Métodos de estudos em biologia da conservação e manejo da vida silvestre. UFPR, Brazil

Scott Jr, N.J. 1982. The herpetofauna of forest litter plots from Cameroon, Africa. Pp. 145-15 in Scott Jr., N.J. (Ed.), Herpetological communities: a symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977. Washington DC: U.S. Fish and Wildlife Service, USA

Shmida, A., and Wilson, M.V. 1985. Biological determinants of species diversity. Journal of Biogeography 12:1-20

Silva, J.M., Rylands, A.B., and Fonseca, G.A.B. 2005. O destino das áreas de endemismo na Amazônia. Megadiversidade 1:124-131

Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology Ecology and Evolution 2:65-79

Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Cerqueira, G.C., Garcia, R.A., Ramos, C.A., Voll, E., Mcdonald, A., Lefebvre, P., and Schlesinger, P. 2006. Modelling conservation in the Amazon basin. Nature 440:520-523

Soininen, J., McDonald, R., and Hillebrand, H. 2007. The distance decay of similarity in ecological communities. Ecography 30:3-12

Soulé, M. 1990. The onslaught of alien species and other challenges in the coming decades. Conservation Biology 4:233-239

Southwell, C.J., Cairns, S.C., Pople, A.R., and Delaney, R. 1999. Gradient analysis of macropod distribution in open forest and woodland of eastern Australia. Australian Journal of Ecology 24:132-143

Sousa, W.P. 1984. The role of disturbance in natural communites. Annual Review of Ecology and Systematics 15:353-391

Stebbins, R.C., and Cohen, N.W. 1995. A Natural History of Amphibians. Princeton University Press, USA

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S., Fischman, D.L., and Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Sullivan, T.P., and Sullivan, D.S. 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. Journal of Applied Ecology 38:1234-1252

Tapia-Coral, S.C., Luizão, F.J., and Wandelli, E.V. 1999. Macrofauna da liteira em sistemas agroflorestais sobre pastagens abandonadas na Amazônia Central. Acta Amazonica 29:477-495

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., and Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79-92

Thiollay, J.M. 1990. Comparative diversity of temperate and tropical forest bird communities: the influence of habitat heterogeneity. Acta Oecologica 11:887-911

Tocher, M.D. 1998. Diferenças na composição de espécies de sapos entre três tipos de floresta e campo de pastagem na Amazônia Central. Pp. 219-232 in Gascon, C., and Moutinho, P. (Eds.), Floresta Amazônica: Dinâmica, regeneração e manejo. Ministério da Tecnologia e Ciência, Brazil

Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. Blackwell Science, United Kingdom

Tuomisto, H., Ruokolainen, K., Kalliola, R., Linna, A., Danjoy, W., and Rodriguez, Z. 1995. Dissecting Amazonian biodiversity. Science 269:63-66

Tuomisto, H., and Ruokolainen, K. 1997. The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. Biodiversity and Conservation 6:347-357

Vasconcelos, T.S., and Rossa-Feres, D.C. 2005. Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do Estado de São Paulo, Brasil. Biota Neotropica 5:1-14

Vitt, L.J., and Caldwell, J.P. 2001. The effects of logging on reptiles and amphibians of tropical forests. Pp. 239-259 in Fimbel, R.A. Grajal, A., and Robinson, J.G. (Eds.), The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, USA

Vonesh, J.R. 2001. Patterns of richness and abundance in a tropical African leaflitter herpetofauna. Biotropica 33:502-510

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:213-251

Wiens, J.A., and Rotenberry, J.T. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21-41

Williams, S.E., Marsh, H., and Winter, J. 2002. Spatial scale, species diversity, and habitat structure: Small mammals in Australian tropical rain forest. Ecology 83:1317-1329

Zar, J.H. 1999. Biostatistical analysis. Prentice-Hall, USA

Zimmerman, B.L. 1994. Audio strip transects. Pp.92-97 in Heyer, W.R. Donnelly, M.A. McDiarmid, R.W. Hayek, L.A.C., and Foster, M.S. (Eds.), Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, USA

Zimmerman, B.L., and Bierregaard, R.O. 1986. Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. Journal of Biogeography 13:133-143

Zug, G.R., Vitt, L.J., and Caldwell, J.P. 2001. Herpetology: an introductory biology of amphibians and reptiles. Academic Press, USA

Capítulo 2

Submetido para a revista *Biotropica*

Species turnover in Amazonian frogs: Low predictability and large differences among terra firme forests

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LRH: Bitar, Tuomisto, Pinheiro, Juen and Santos-Costa

RRH: Partitioning Amazonian Anuran Turnover

Species turnover in Amazonian frogs: Low predictability and large differences among terra firme forests

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Abstract

Species distributions and the factors explaining them at different spatial scales have been intensively studied recently, but within Amazonia, most such studies have focused on plants. Less attention has been paid to animals, for which it is not as obvious which environmental variables should be considered potentially relevant. Our aim is to understand the determinants of anuran turnover in Amazonian *terra-firme* forests and how the perception of these may change among regions and across spatial scales. We sampled frogs in 56 plots distributed in ponds and streams over three *terra-firme* forest areas in Eastern Amazonia. Using multiple regressions with distance matrices, we partitioned the variation in species turnover into components explained by variation in environmental and spatial distances. This was done in parallel for each area separately and for all areas together in order to assess how consistent the results are between scales and across areas at the same scale. Each community seemed to respond to a set of factors specific to that area, and the identity of the variables that emerged as significant were different among areas and scales. Both geographical distances and environmental differences had larger explanatory power at the regional scale than at the local scale. The total explanatory power was R^2=42.1% at the regional scale, and varied between R^2=3.5% and R^2=36.2% at the local scale. The large differences among the results obtained for different areas caution against making broad generalizations about species turnover patterns from one community to others, as real differences may exist among areas.

Key-words Amazonia; Anurans; beta diversity; variation partitioning; species distribution; spatial auto-correlation; tropical forest

SPECIES ARE NOT DISTRIBUTED UNIFORMLY ON THE LAND SURFACE, AND THE REASONS leading to this have long intrigued scientists. Because species are thought to have adapted to different environments, it is logical to expect that there will be community-wide species turnover along the environmental gradients that are most important for the organisms (Whittaker 1956, Parris 2004, Keller *et al.* 2009). For example, species turnover along altitudinal gradients in montane landscapes has been described for birds (Terborgh 1973, Jankowski *et al.* 2009), moths (Brehm *et al.* 2003) and amphibians (Poynton *et al.* 2007).

Within lowland tropical rainforests, habitat variation is less obvious than in mountainous areas. Nevertheless, high ecological heterogeneity and floristic differences related to differences in soil properties among sites have been documented also in the Amazonian lowlands (Tuomisto and Ruokolainen 1997, Phillips et al. 2003, Tuomisto et al. 2003a,b,c, Normand et al. 2006, Ruokolainen et al. 2007). This may increase species turnover over broad spatial scales. It is more difficult to identify a universally relevant set of environmental variables for animals than for plants, because animal species differ in their use of dietary resources and reproductive habitat. For example, compositional similarity has been related to differences in rainfall, length of the dry season and flooding depth in a study on ants spanning a large and environmentally heterogeneous area in Amazonian lowland (Vasconcelos *et al.* 2010). In western Amazonia, bird species turnover was found to correlate with plant species turnover and variation in soils (Pomara et al. 2012). The difficulty in establishing a universal subset of environmental predictors of animal distributions has led to mixed results that are difficult to compare with each other. In the case of frog studies, different studies have given importance to at least canopy cover or vegetation structure (Crump 1971, Halverson *et al.* 2003, Souza *et al.* 2008, Provete et al. 2014), air temperature and humidity (Crump 1971, Vonesh 2001, Haddad & Prado 2005), water availability (Zimmerman & Bierregaard 1986) and litter volume and depth (Giaretta *et al.* 1999).

There is some indication that species richness of Amazonian frogs may be similar to that in lowland New Guinea at the local scale, but species turnover in Amazonia may be higher (Dahl et al. 2009). In the present study, we aim to clarify what the species turnover patterns of Amazonian anurans are, and which external variables they are related to. Brazilian Amazonia is known to harbor at least 221 frog species (Ávila-Pires *et al.* 2007). Many species appear to be highly dependent on specific aspects of the environment, such as appropriate conditions of aquatic/humid habitats for reproduction and foraging (Stebbins & Cohen 1995, Zug *et al.* 2001). Anurans have two distinct life stages, tadpoles and adults. Tadpoles usually develop in water, and they may be even more susceptible to changes in water temperature, solar radiation, food resource and specific microhabitats than adults are (Provete et al. 2014). In one study, aquatic breeders were found to show high dependence on the availability and characteristics of waterbodies, whereas the distributions of terrestrially breeding species seemed to be more spatially than environmentally structured (Landeiro et al. 2014).

In Amazonia, riparian forests have been found to have more species and a different species composition when compared to non-riparian forests (Ribeiro *et al.* 2012, Menin *et al.* 2011). Frog species composition can also change between isolated ponds and streamside ponds (Rodrigues *et al.* 2010). Disturbances that change habitat characteristics in Amazonian transitional forest may select for species with reproduction modes adapted to open areas (Bitar et al. 2012) and decrease species turnover (Bitar *et al.* 2015). The studies carried out so far have differed from one another in sampling scales (grain and extent), field protocols, developmental stages considered (adults vs. tadpoles) and the breeding modes of the target species (leaf-litter, aquatic or terrestrial breeding). Such differences make it difficult to draw general conclusions from the results.

Changes in grain (size of the sampling units) and extent (size of the total area sampled) of a study have a direct effect on the results (Arrhenius 1921, Palmer & White 1994, Nekola & White 1999, Whittaker *et al.* 2001, Steinbauer *et al.* 2012, Barton *et al.* 2013). If grain size is very small, turnover increases due to stochastic variation and is, hence, difficult to relate to ecological gradients (high noise-to-signal ratio). If grain size is very coarse, each sampling unit becomes internally so heterogeneous that species–environment relationships become difficult to detect (Tuomisto 2010, Steinbauer *et al.* 2012, Barton *et al.* 2013). Increasing the extent of a study also extends the environmental gradients included in the analyses, and may cause entirely new habitats to be included. Because grain and extent have such a strong effect on the observed species turnover, they need to be chosen according to the spatial structure of the environmental variables of interest and how the organisms of interest perceive their environment (Barton *et al.* 2013). For example, climatic and historical (evolutionary) factors generally vary over the landscape very gradually, and observing them necessitates a large study extent. In contrast, many aspects of habitat structure can vary sharply over short distances, which can only be observed if the study grain is sufficiently small.

In addition, dispersal limitation and historical factors may cause species turnover among geographically separated sites of similar environments (Nekola & White 1999). Nearby sites have been found to have more similar ant, bird, anuran and reptile faunas than more distant sites in Amazonia (Ernst & Rodel 2008, Vasconcelos *et al.* 2010, Calderon-Patron *et al.* 2013). Such a pattern can be due to limited species dispersal ability, spatial autocorrelation in the important environmental variables, or a combination of both.

The purpose of the present study is to obtain new understanding of the determinants of anuran species turnover in Amazonian *terra-firme* rain forests, and how the perception of these determinants may change across spatial scales and among regions. To achieve these goals, we apply a standard sampling methodology in three different areas of relatively uniform and well-preserved Amazonian forest, with a maximum distance among areas of almost 600 km.

METHODS

Study area — Field surveys were conducted in three terra-firme (non-inundated) sites within lowland Amazonian rainforests. All sites were in conservation units (National Forest, NF), and had a continuous cover of old-growth forest: Amapá NF, Tapajós NF and Caxiuanã NF. Amapá NF is located on the Guiana shield in the State of Amapá, between the Falsino and Araparí rivers (Fig. 1A). The other two areas are south of the Amazon river, Caxiuanã NF in the Xingu–Tocantins interfluve in the east (Fig. 1B), and Tapajós NF further west between the Tapajós and Xingú rivers (Fig. 1C). All sites are considered to represent terra-firme forests, but there are differences in altitude, temperature and precipitation among them (Table 1).

[Insert Table 1]

[Insert Figure 1]

EXPERIMENTAL DESIGN — Fieldwork was done during the same rainy season in all three sites, between January and April 2011. Expeditions lasted 26 days on average, and we established 20, 19 and 17 plots in Amapá, Caxiuanã and Tapajós, respectively. Each plot was 2100 m² in size (70 m x 30 m) and separated by a distance of at least 500 m from the nearest other plot. The maximum distance (local extent) between plots was 8.8 km in Amapá (mean pairwise distance=3 km), 28.2 km in Caxiuanã (mean=13.1 km) and 15.5 km in Tapajós (mean=3.9 km). The plots were placed such that each incorporated a watercourse in a way that all plots are located in terra firme forests with no more than half of its area covered by water (streams or ponds). The presence of water is already considered one of the most important environmental factors for anurans (Zimmerman & Bierregard 1986), and we aimed to answer more specific qustions about how important the different properties of waterbodies are.

In the Amapá plots, 60% of watercourses were lotic, with average water velocity of 0.13 m/s (). Most streams were narrow (4.2 m average, ranging from 1m to 23.5m), with sandy bottom, clear water and little deposition of organic matter (mainly dry leaves). In Caxiuanã, approximately 85% of the watercourses were lentic (without water flow), 30.4 m of mean width (2.9 m minimum and maximum width greater than 50m), with high deposition of organic material and abundant vegetation in the water. In the Tapajós plots, almost all watercourses were lotic (88%), average water width of 19.4 m (3.9m minimum and approximately 40m maximum width) and average water velocity of 0.24 m/s.

Plot boundaries were marked with string. Within them, active visual encounter surveys and auditory surveys were carried out simultaneously (Crump & Scott 1994, Zimmerman 1994, Menin *et al.* 2007). Searches were conducted twice in each plot

(Zimmerman 1994, Crump & Scott 1994), once during the day (between 14:00h and 18:00h) and once during the night (between 20:00h and 24:00h). During each period, three collectors walked side by side for at least 2 hr, or until no new frog individuals were recorded. All frog individuals that were either sighted or heard calling inside the plot were identified to species and counted. Whenever possible, the sighted individuals were captured and kept away from the plot to avoid recounting the same specimens. Most individuals were released at the end of the night survey, but at least one individual of each species was collected for later confirmation of species identifications. This also made it possible to standardize the morphospecies classifications among all study areas when identification into species level was not possible due to taxonomical uncertainties.

ENVIRONMENTAL VARIABLES — In each plot we measured eleven environmental variables that specifically describe the environment of the watercourses and their surroundings, based on protocols of Peterson (1992) and Barbour *et al.* (1999). The variables were: margin profile, margin type, water surface covered by vegetation, hydroperiod, margin substrate, margin vegetation, flow obstruction forming dams (presence and kind of material obstructing water flow), ravine, channel bottom type (kind of material present on the bottom of the watercourse channel), aquatic vegetation and debris. The variables are described in more detail in Appendix S1. A single observer (always the same) covered the approximate distance of 30m along the watercourse and the protocol was filled taking into account what was observed in this stretch. For each plot a protocol was filled only once.

In addition, we also measured another eleven variables in each plot: day temperature (ºC), night temperature (ºC), daytime air moisture (%), nighttime air moisture (%), canopy openness (%), litter depth (cm), watercourse width (m), watercourse depth (cm), water velocity (m/s), mean CBH (tree circumference at breast height - mm) and the number of tree stems. Two temperature and moisture measurements were taken in each plot, once during the day survey and once during the night survey. A digital thermohygrometer (Instrutherm, model HT-270) was used for this purpose. Canopy openness (%) is based on the average of four hemispherical photos per plot taken with a digital camera attached to a tripod 50cm above the ground. The photographs were analyzed with the program ENVI 4.5 (ITT Visual Information Solutions, Boulder, Colorado, USA). Litter depth was measured at four points within each plot. Usually there was one measurement point in each corner, but if any of these points was affected by a waterbody, the measurement was taken from the middle of the plot instead. The average of the four values was used in the analyses. Water velocity was measured during the day survey, by timing how many seconds it took a piece of Styrofoam to travel one meter in the fastest point of the watercourse. Width and depth measurements were taken with a tape measure at the widest or deepest point of the watercourse, respectively. Number of tree stems and mean CBH were measured in two sub-plots (5m x 10m) located at opposite corners within the plot. All woody plants with CBH ≥ 5cm inside the sub-plots were taken into account.

STATISTICAL ANALYSES — We assessed general faunistic similarity between areas with the Sørensen similarity index. This is based on presence/absence of species and ranges from zero (no shared species) to one (identical species compositions). Species turnover was calculated between all possible pairs of plots using the Bray-Curtis dissimilarity index. Species abundances were log-transformed before calculating the index values in order to lessen the weight given to extremely abundant species. Environmental dissimilarity matrices were calculated separately for each environmental variable to allow assessing their relative explanatory powers in multiple regression. Euclidean distance was used for the quantitative variables and Gower distance for the categorical ones (margin profile, hydroperiod, margin types, margin vegetation and ravine; Appendix S1).The following environmental variables were log-transformed before calculating the dissimilarities: day moisture, night moisture, canopy cover, litter depth, CBH, tree abundance, water width and water depth. Geographical distance matrices were calculated on the basis of plot coordinates obtained with hand-held GPS receivers in the field.

We used non-Metric Multidimensional Scaling (NMDS) to illustrate the compositional dissimilarity patterns in an ordination diagram (Legendre & Legendre 2012). To assess the relative contributions of geographical distances and the 22 environmental dissimilarity matrices to explaining variaiton in species turnover, we used multiple regression on distance matrices (MRM; Tuomisto *et al.* 2003c, Lichstein 2007). We first made an initial selection of the explanatory variables by running the regression analyses with each dissimilarity matrix separately. Those environmental variables that were found significant on their own were used to build an initial MRM model. The model was then simplified, and the covariation among explanatory variables reduced, by using backward elimination until the final MRM model (MRM_{env}) contained only those explanatory variables that made a significant ($p<0.05$) partial contribution to explaining species turnover. If the model containing only the geographical distance matrix (MRM_{geo}) was significant, an additional MRM containing all variables from both MRM_{env} and MRM_{geo} was run (MRM_{all}). The R^2 values of the three MRM models were then used to estimate the proportion of variance in species turnover that was uniquely explained by environmental dissimilarities (MRM_{all} – MRM_{geo}), uniquely explained by geographical distances (MRM_{all} – MRM_{env}) and jointly explained by both groups of variables (MRM_{geo} + MRM_{env} – MRM_{all}). We assessed statistical significance using a Monte Carlo permutation test with 10000 permutations.

All analyses were carried out both at the local scale (dissimilarity matrices constructed for each of the three areas separately) and at the regional scale (all plots from all three areas combined into one dissimilarity matrix). The analyses were performed in R using the packages cluster (Maechler *et al*. 2013) and ecodist (Goslee & Urban 2007).

RESULTS

SPECIES TURNOVER — We registered 948 frog individuals representing 40 species in Amapá, 819 individuals of 26 species in Caxiuanã and 923 individuals of 32 species in Tapajós. In total, there were 65 species in the three sites together, of which 21 were only found in Amapá, four only in Caxiuanã and 12 only in Tapajós; five species were shared by all areas (Appendix S2). Overall compositional similarity was highest between Amapá and Tapajós (Sørensen index 0.69) and lowest between Caxiuanã and Tapajós (0.52), with Amapá and Caxiuanã intermediate (0.61). The most species-rich family in every area was Hylidae (28 species in all areas together), followed by Leptodactylidae (nine species) and Bufonidae (seven species).

The area with the highest between-plot species turnover was Amapá (mean Bray-Curtis dissimilarity 0.71, range 0.28 – 1), then Caxiuanã (mean 0.61, range 0.25 – 1) and Tapajós (mean 0.53, range 0.18 – 0.82) (Fig. 2). As could be expected, mean species turnover increased when data from all three sites were combined (mean Bray-Curtis dissimilarity 0.76, range 0.18 – 1), but the difference between this regional scale and the local scale within Amapá was relatively small. The percentage of plot pairs that shared no frog species was only 8.3% in the entire dataset, 7.9% in Amapá, 3.5% in Caxiuanã and zero in Tapajós. This means that our data do not suffer from the dissimilarity saturation problem that could distort MRM and other analysis results (Tuomisto *et al.* 2012).

In the NMDS ordination containing all sites (Fig. 2A), the inventory plots were clearly aggregated according to their position in geographical space. This indicates that there is geographical differentiation in frog species composition across the three sites. Fifteen of the 22 environmental variables were significantly correlated with NMDS ordination axes at the regional scale, seven in Amapá, none in Caxiuanã and two in Tapajós (Fig. 2).

[Insert Figure 2]

VARIATION IN SPECIES TURNOVER EXPLAINED BY ENVIRONMENTAL AND SPATIAL DISTANCES — Regional scale: At the extent of the entire study, dissimilarities in ten of the measured environmental variables made a statistically significant contribution to explaining variation in anuran species turnover (Table 2). These were not always the variables that showed most variation in relative terms (Tables 2 and 3). All the significant variables can be considered to represent suitability of the local conditions for oviposition and tadpole development. This is the case especially with air temperature and watercourse conditions for the aquatic breeders, and with air moisture for the terrestrial and vegetation breeders. Differences in day and night moisture explained the variation in anuran species turnover best, with R^2 values of 16.9% and 10.1%, respectively, followed by differences in watercourse width (R^2=7.8%) and channel bottom type (R^2=5.4%).

[Insert Table 2]

The MRM model with the environmental variables obtained after backward elimination (MRM_{env}) retained day moisture, watercourse width, channel bottom type, margin profile, margin type and hydroperiod (Table 2). Together with geographical distances (MRM_{all}), dissimilarities in these variables explained 42.1% of the total variation in anuran species turnover ($p<0.01$). Variance partitioning showed that environmental and geographical distances made approximately equal contributions at the regional scale, and that the shared fraction was only marginally larger than the uniquely environmental and uniquely geographical fractions (Fig. 3A).

[Insert Figure 3]

[Insert Table 3]

Local scale: When the three sites were analyzed separately, MRM yielded rather different results in each, both in terms of which explanatory variables were selected in the final model and in terms of the obtained R^2 values. Species turnover was related to the differences in seven environmental variables in Amapá, but only two in Caxiuanã and four in Tapajós (Table 2). From the 22 measured variables, eight are not related to waterbody characteristics, and of these only temperature and air moisture proved to be significant in Amapá (daytime and nighttime air moisture) and Tapajós (night temperature and daytime air moisture). These variables are important environmental conditions for anurans with terrestrial oviposition. In Caxiuanã, both significant variables (margin type and margin substrate) were related to characteristics of the ponds and streams (Table 2). None of the explanatory variables was significant in all three areas, but three (geographical distance and differences in daytime air moisture and watercourse width) were significant in both Amapá and Tapajós, and one (difference in margin substrate) was significant in both Amapá and Caxiuanã.

The variance partitioning results yielded relatively similar fractions explained by environmental and geographical distances for Amapá and Tapajós (Figure 3B, D) but very different results for Caxiuanã (Fig. 3C). All significant variables together (MRM_{all}) explained 36.2% of the total variance in species turnover in Amapá and 30.0% in Tapajós, but only 3.5% in Caxiuanã. In all sites, the purely environmental fraction was the largest. In Caxiuanã, the spatial component was not even statistically significant (MRM_{geo} R^2=0.9%, p=0.13). The purely environmental fraction was higher both in Amapá (24.8%) and in Tapajós (22.2%) than in the analysis combining all three sites (11.9%). The opposite was true for the fractions involving geographical distances, which were largest in the regional analysis (Fig. 3). Especially the purely spatial fraction was small at the local scale (2.7% in Amapá, 0.3% in Tapajós and not significant in Caxiuanã).

DISCUSSION

LOCAL-SCALE SPECIES TURNOVER — Since our study sites consisted of apparently similar well-preserved Amazonian *terra-firme* forest, our prior expectation was that they would also yield similar results on the factors that explain anuran community turnover. However, this was only partly the case, which made it evident that factors that may affect species communities vary even inside this forest habitat. Differences in local environmental characteristics were more important than geographical distances in explaining the variation in anuran species turnover at all sites. However, the set of environmental distances retained in the final MRM model consisted of different variables in each site: daytime air moisture, watercourse width and channel bottom type in Amapá; daytime air moisture, night temperature and water vegetation in Tapajós; and only margin type in Caxiuanã. These differences were observed even though grain and extent were kept the same in all sites, and the sampling was planned so as to ensure that a water body was present in all plots.

A recurring problem when comparing results from separate studies is how to interpret differences in their results. For example, Ernst and Rödel (2008) studied spatial and environmental effects on frog species turnover, just as we did, but in contrast to us, they concluded that "environmental factors did not prove to be significant predictors of species incidence in any of the assemblages analysed". Such differences may emerge from at least four kinds of causes. Firstly, it is possible that there are real differences among areas in how well the species distributions reflect present-day environmental variability. For example, there may be historical legacies or interspecific interactions that cause species turnover patterns to differ from what would be expected on the basis of the environment alone. Such effects may be behind the differences among our study areas: although we measured the same variables in all three, in one of our sites (Caxiuanã) their explanatory power was much less than in the other two. Differences in this respect between our study and the study by Ernst and Rödel (2008) are potentially even greater, as ours was made in eastern Amazonia and theirs in French Guiana and Côte d'Ivoire (West Africa).

Secondly, differences among studies can depend on what was actually measured in the field. Some of the differences between our study and Ernst and Rödel (2008) may reflect the fact that they focused on different environmental variables than we did, and they did not measure some of the variables that emerged as important in our study (air temperature, air moisture, water width and some other water body properties).

Thirdly, differences among studies may depend on how the data were analyzed. Ernst and Rödel (2008) summarized all environmental variables into a single distance matrix, instead of using each one separately. As in any regression analysis, combining several explanatory variables into a single simplified index generally reduces the total amount of variance that can be explained. This is especially the case if some of the variables have little or no explanatory power, as then they just add noise to the index value.

Finally, the sampling setup may be different. Ernst and Rödel (2008) used 600-m-long transects subdivided into 24 contiguous sampling units, which provided a systematic sample of a rather small area. In contrast, our sampling kept one aspect of the environment fixed (all sampling units contained a water body) but otherwise attempted to capture a representative sample of the local environmental heterogeneity by separating the sampling units by at least 500m from each other.

Although one aim in ecological research is to find generally applicable principles (Tews et al 2004), achieving this is not easy. The amphibian communities in our three study areas did not give similar results, even though their environments were a priori expected to be similar, and the scales of observation were also similar. Rather than discovering a set of generally applicable predictors of anuran species turnover, we found that different environmental filters appeared important in different places, and also the degree to which species turnover was predictable varied. In two of the areas, our results paralleled those of Keller et al. (2009) from Borneo: variation in species turnover was better explained by environmental variables than by spatial distances.

In our study, only a small part of the variation in species turnover could be explained by geographical distances at the local scale. At the regional scale, the fraction of variance jointly explained by environmental and geographical distances was relatively large, indicating that there was a spatial gradient in the environmental variables themselves. This contrasts with the results of Ernst & Rödel (2008). Although the extent of their study areas was similar to ours (20 km^2 in Amazonia and 30 km^2 in Africa), they found that compositional dissimilarities and geographical distances were correlated in all communities they studied.

Several studies have carried out analyses similar to ours in order to assess the factors behind plant species turnover in Amazonia (Phillips *et al.* 2003, Tuomisto *et al.* 2003a,b,c; Normand *et al.* 2006, Ruokolainen *et al.* 2007). Their results have also varied, especially in the relative importance given to geographical distances vs. environmental differences. For example, a study that compared three areas in western Amazonia using a standardized field methodology and uniform spatial grain (Ruokolainen *et al.* 2007) found that the environmental variables were most important in those areas where their sampled gradients were longest. In our data, there was a similar tendency: any given variable was most likely to be significant in the sites where its coefficient of variation was highest. However, this pattern did not hold across variables, i.e. a long sampled gradient did not guarantee that a variable emerged as significant in the analyses.

Finally, why were the results we obtained in Caxiuanã so different from those in the other sites? One possibility is that this region has a physiographic feature not found in the other studied areas, namely ria lakes (Montag *et al.* 2013). These are lentic water bodies that form when a river becomes dammed and its valley drowned either by the geological process of aggradation or because of a rise in the sea level (Hida *et al.* 1999, Behling & Costa 2000). Due to their currently lentic nature, the limnological characteristics of ria lakes are more similar to lakes than to rivers (Sioli 1984, IBGE 1991, Montag & Barthem 2006). The resulting changes in the physicochemical characteristics of the water may influence anuran species distributions and other community characteristics in ways that are not related to the variables that we measured in the present study. Even if the differences depended on some other factor, it is obvious that Amazonia cannot be considered uniform for frogs at the regional scale, and its heterogeneity needs to be taken into account when comparing results from separate sites.

ACROSS-SCALE COMPARISONS — The three sites included in our study were located rather far from each other, so differences in anuran community composition among them were not entirely unexpected. Indeed, at the broad scale (when data from the three study areas were combined), there was more compositional heterogeneity (mean species turnover between plots was higher) than at the local scale (within any of the three areas). The observed environmental gradients were also longer. The higher heterogeneity may have led to a smaller noise-to-signal ratio in the data, which could at least partly explain the higher R^2 values of the MRM models at the regional scale (42%) than at the local scale (3.5–36.1%). The regional scale analyses also identified more environmental variables as significant than any of the local-scale analysis did, as most of the variables that had been identified as significant in one of the sites remained significant in the combined data. The variables with the highest explanatory power were air moisture (during both day and night), watercourse width and channel bottom type, which are related to the availability of reproductive habitats for frogs.

In our regional data, the largest explained fraction of variation in frog turnover (16.9% in a total of 42.1%) was jointly explained by geographical and environmental distances. Provided that all the relevant environmental variables have been measured (which is by no means certain), the fraction explained exclusively by geographical distances (13.2%) can be interpreted in terms of the effect of dispersal limitation, which is considered stronger in anurans than in other vertebrates (Smith & Green 2005, Qian 2009). Although environmental processes do not lead to similar patterns in all *terra-*

firme sites, we highlight the importance of both processes together, environmental and geographical distance, to explain the variation in amphibian communities. It is also obvious that varying the scale of observation is linked to different effect sizes of each partition.

CONCLUSIONS — We addressed species turnover patterns in anuran communities at local and regional scales in Amazonia, and found that results can vary considerably not only among spatial scales but also among areas sampled at the same scale. Differences concerned both the identity of the variables chosen as significant in MRM models and the proportion of variance in species turnover that the variables were able to explain. Both geographical distances and environmental differences had larger explanatory power at the regional scale (large extent) than at the local scale (small extent). However, other factors than extent of the study area must have been important even in this relatively uniform Amazonian environment, because anuran species turnover showed such different patterns in each of the three study sites. It seems that each community is responding to a set of factors specific to that site, and further studies are needed to clarify what these factors might be. Furthermore, the proportion of unexplained variance in our analyses was relatively large. This leaves room to speculate if we missed important environmental or historical variables, or if a large part of the species turnover is, in fact, due to stochastic variation and is, therefore, inherently unpredictable. In any case, our results caution against making sweeping generalizations from one community to others, as real differences seem to exist among sites.

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References

ANGERMEIER, P. L., AND J. R. KARR. 1984. Fish communities along environmental gradients in a system of tropical streams. *In* T. M. ZARET (Eds.). Evolutionary ecology of neotropical freshwater fishes, pp. 39-57. Netherlands, Dr. W. Junk Publishers.

ARBELÁEZ, F., J. F. DUIVENVOORDEN, AND J. A. MALDONADO-OCAMPO. 2008. Geological differentiation explains diversity and composition of fish communities in *terra-firme* streams in the southern Amazon of Colombia. J. Trop. Ecol. 24: 505-515.

ARRHENIUS, O. 1921. Species and area. J. Ecol. 9: 95–99.

ÁVILA-PIRES, T. C. S., M. S. HOOGMOED, AND L. J. VITT. 2007. Herpetofauna da Amazônia. *In* L. B. NASCIMENTO, AND M. E. OLIVEIRA. (Eds.). Herpetologia no Brasil II, pp. 13-43. Sociedade Brasileira de Herpetologia, Belo Horizonte, Brasil.

BARROS, D. F., A. L. M. ALBERNAZ, J. ZUANON, H. M. V. ESPÍRITO SANTO, F. P. MENDONÇA, AND A.V. GALUCH. 2013. Effects of isolation and environmental variables on fish community structure in the Brazilian Amazon Madeira-Purus interfluve. Braz. J. Biol. 73: 491-499.

BARTON, P. S., S. A. CUNNINGHA, A. D. MANNING, H. GIBB, D. B. LINDENMAYER, AND R. K. DIDHAM. 2013. The spatial scaling of beta diversity. Global Ecol. Biogeogr. 22: 639–647.

BEHLING, H. AND M.L. COSTA. 2000. Holocene Environmental Changes from the Rio Curuá Record in the Caxiuana Region, Eastern Amazon Basin. Quaternary Res. 53: 369-377.

BITAR, Y. O. C., L. P. C. PINHEIRO, P. S. ABE, AND M. C. SANTOS-COSTA. 2012. Species composition and reproductive modes of anurans from a transitional Amazonian forest, Brazil. Zoologia, 29: 19-26.

BITAR, Y. O. C., L. JUEN, L. P. C. PINHEIRO AND M. C. SANTOS-COSTA. 2014. Anuran Beta Diversity in a Mosaic Anthropogenic Landscape in Transitional Amazon. J. Herpetol. In-Press.

BREHM, G., J. HOMEIER, AND K. FIEDLER. 2003. Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. Divers. Distrib. 9: 351-366.

BUCKLEY, L. B. AND W. JETZ. 2007. Environmental and historical constraints on global patterns of amphibian richness. P. R. Soc. B. 274: 1167-1173.

L. B. BUCKLEY, AND W. JETZ. 2008. Linking global turnover of species and environments. PNAS. 105: 17836–17841.

CALDERÓN-PATRÓN, J.M., C. E. MORENO, R. PINEDA-LÓPEZ, G. SÁNCHEZ-ROJAS, AND I. ZURIA. 2013. Vertebrate Dissimilarity Due to Turnover and Richness Differences in a Highly Beta-Diverse Region: The Role of Spatial Grain Size, Dispersal Ability and Distance. PLoS ONE. 8:e82905.

CAREY, C. AND M. A. ALEXANDER. 2003. Climate change and amphibian declines: is there a link? Divers. Distrib. 9: 111–121.

CINTRA, R., W. E. MAGNUSSON, AND A. L. ALBERNAZ. 2013. Spatial and temporal changes in bird assemblages in forest fragments in an eastern Amazonian savanna. Ecol. Evol. 3: 3249-3262.

COLVILLE, J., M. D. PICKER, AND R. M. COWLING. 2002. Species turnover of monkey beetles (Scarabaeidae: Hopliini) along environmental and disturbance gradients in the Namaqualand region of the succulent Karoo, South Africa. Biodivers. Conserv. 11: 243-264.

CRUMP, M.L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. Occasional Papers Museum of Natural the University of Kansas, USA, pp. 62.

CRUMP, M.L. AND N. J. SCOTT JR. 1994. Visual encounter surveys. *In* W. R. HEYER, M. A. DONNELLY, R. W. MCDIARMID, L. A. C. HAYEK, AND M. S. FOSTER. (Eds.). Measuring and monitoring biological diversity: standard methods for amphibians, pp. 84-92. Washington DC: Smithsonian Institution Press.

DIDHAM, R.K., P. M. HAMMOND, J. H. LAWTON, P. EGGLETON, AND N. E. STORK. 1998. Beetle species responses to tropical forest fragmentation. Ecol. Monogr. 68: 295-323.

DONNELLY, M. A. 1998. Potential effects of climate change on two neotropical amphibian assemblage. Climatic change. 39: 541-561.

DUELLMAN, W. E. 2005. Cusco Amazónico – the lives of amphibians and reptiles in an Amazonian rainforest. Cornell: University Press, pp. 433.

ERNST, R., T. KONRAD, K. E. LINSENMAIR, AND M. O. RÖDEL. 2007. The impacts of selective logging on three sympatric species of Leptodactylus in a Central Guyana rainforest. Amphibia-Reptilia. 28: 51-64.

ERNST, R. AND M. O. RÖDEL. 2008. Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environmental effects in disturbed and undisturbed forests. J. Trop. Ecol. 24: 111-120.

GIARETTA, A. A., K. G. FACURE, J. H. M. MEYER, AND N. CHEMIN. 1999. Diversity and abundance of litter frogs in a forest of southeastern Brazil: seasonal and altitudinal changes. Biotropica. 31: 669-674.

GOSLEE, S. C. AND D. L. URBAN. 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Stat. Software 22:1-19.

HADDAD, C. F. B. AND C. P. A. PRADO. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil. BioScience. 55: 207-217.

HALVERSON, M.A., D.K. SKELLY, J.M. KIESECKER, AND L.K. FREIDENBURG. 2003. Forest mediated light regime linked to amphibian distribution and performance. Oecologia. 134: 360-364.

HARTEL, T., S. NEMES, L. DEMETER, AND K. ÖLLERER. 2008. Pond and landscape characteristics—which is more important for common toads (Bufo bufo)? A case study from central Romania. Appl. Herpetol. 5: 1–12.

HIDA, N., J. G. MAIA, M. HIRAOKA, O. SHIMM, AND M. NOBUAKI. 1999. River water level changes of the Amazon Estuary: at Breves, Caxiuanã and Abaetetuba. Manaus'99 - Hydrological and Geochemical Processes in Large Scale River Basins. pp. 1-9.

IBGE - Instituto Brasileiro de Geografia e Estatística. 1991. Geografia do Brasil v.3: Região Norte. Série Geografia do Brasil. Rio de Janeiro, pp. 307.

JANKOWSKI, J.E., A. L. CIECKA, N. Y. MEYER, AND K. N. RABENOLD. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. J. Anim. Ecol. 78: 315-327.

JUEN, L. AND P. JR. DE MARCO. 2011. Odonate beta diversity in terra-firme forest streams in Central Amazonia: On the relative effects of neutral and niche drivers at small geographical extents. Ins. Conserv. Divers. 4: 265-274.

KELLER, A., M. O. RÖDEL, K. E. LINSENMAIR, AND T. U. GRAFE. 2009. The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. J. Anim. Ecol. 78: 305-314.

LEGENDRE, P., F. LAPOINTE, AND P. CASGRAIN. 1994. Modeling brain evolution from behavior: A permutational regression approach. Evolution. 48: 1487-1499.

LEGENDRE, P. AND L. LEGENDRE. 1998. Numerical Ecology. 3nd English edition. Elsevier Science, Amsterdam.

LICHSTEIN, J. 2007. Multiple regression on distance matrices: A multivariate spatial analysis tool. Plant Ecol. 188: 117-131.

MAECHLER, M., P. ROUSSEEUW, A. STRUYF, M. HUBERT, AND K. HORNIK. 2013. cluster: Cluster Analysis Basics and Extensions. R package version 3.1.0.

MANLY, B. F. J. 1986. Randomization and regression methods for testing for associations with geographical, environmental and biological distances between populations. Researc. Pop. Ecol. 28: 201-218.

MENDONÇA, F. P., W. E. MAGNUSSON, AND J. ZUANON. 2005. Relationships between habitat characteristics and fish assemblages in small streams of central Amazonia. Copeia. 4: 751-764.

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. 17: 86-91.

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.

MEZGER, D. AND M. PFEIFFER. 2011. Partitioning the impact of abiotic factors and spatial patterns on species richness and community structure of ground ant assemblages in four Bornean rainforests. Ecography. 34: 39-48.

MONTAG, L. F. A. AND R. B. BARTHEM. 2006. Estratégias de Conservação em Comunidades de Peixes da Bacia de Caxiuanã (Melgaço/PA): Um Lago Antigo a ser Comparado com Represas Novas. Bol. Socied. Brasil. Ictio. 82: 4-5.

MONTAG, L. F. A., T. M. S. FREITAS, N. L. BENONE, C. P. FERREIRA, W. B. WOSIACKI, AND R. B. BARTHEM. 2013. Ecologia de peixes em um “quase-lago” da Amazônia Oriental. *In* LISBOA, P. L. B. (Ed.). Caxiuanã: paraíso ainda preservado, pp. 577-593. Belém: Museu Paraense Emílio Goeldi.

MOULATLET, G. M., F. R. C. COSTA, C. D. RENNÓ, T. EMILIO, AND J. SCHIETTI. 2014. Local Hydrological Conditions Explain Floristic Composition in Lowland Amazonian Forests. Biotropica. 46: 395-403.

NEKOLA, J. C. AND P. S. WHITE. 1999. The distance decay of similarity in biogeography and ecology. J. Biogeogr. 26: 867–878.

NORMAND, S., J. VORMISTO, J. C. SVENNING, C. GRÁNDEZ, AND H. BALSLEV. 2006. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. Plant Ecol. 186: 161–176.

PALMER, M. W. AND P. S. WHITE. 1994. Scale dependence and the species-area relationship. Americ. Natur. 144: 717-40.

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

PETERSEN, R. C. JR. 1992. The RCE: a riparian, channel, and environmental inventory for small streams in agricultural landscape. Freshwater Biol. 27. 295-306.

PHILLIPS O.L., P. VARGAS NÚÑEZ, A. MONTEAGUDO LORENZO, A. CRUZ-PEÑA, M. E. ZANS CHUSPE, W. SÁNCHEZ GALIANO, M. YLI-HALLA, AND S. ROSE. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. J. Ecol. 91: 757–775.

PLAFKIN, J.L., M. T. BARBOUR, K. D. PORTER, S. K. GROSS, AND R. M. HUGHES. 1989. Rapid Bioassessment Protocols for Use in Streams and Rivers: Benthic Macroinvertebrates and Fish. United States Environmental Protection Agency, EPA, 444/4-89-001, Washington DC.

POMARA, L. Y., K. RUOKOLAINEN, H. TUOMISTO, AND K. R. YOUNG. 2012. Avian composition co-varies with floristic composition and soil nutrient concentration in Amazonian upland forests. Biotropica. 44: 545-553.

POMARA, L. Y., K. RUOKOLAINEN, AND K. R. YOUNG. 2014. Avian species composition across the Amazon River: the roles of dispersal limitation and environmental heterogeneity. J. Biogeogr. 41: 784-796.

POYNTON, J. C., S. P. LOADER, E. SHERRATT, AND B. T. CLARKE. 2007. Amphibian diversity in East African biodiversity hotspots: altitudinal and latitudinal patterns. Biodiv. Conserv. 16: 1103-1118.

QIAN, H. 2009. Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. J. Syst. Evol. 47: 509–514.

QIAN, H. AND R. E. RICKLEFS. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. Global Ecol. Biogeogr. 21: 341–351.

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

RODRIGUES, D.J., A. P. LIMA, W. E. MAGNUSSON, AND F. R. C. COSTA 2010. Temporary pond availability and tadpole species composition in Central Amazonia. Herpetologica. 66: 124-130.

RUOKOLAINEN, K., H. TUOMISTO, M. J. MACIA, M. A. HIGGINS, AND M. YLI-HALLA. 2007. Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? J. Trop. Ecol. 23: 13-25.

SIOLI, H. 1984. The Amazon and its main affluents: Hydrography, morphology of the river courses, and river types. *In* SIOLI, H. (Ed.).The Amazon: limnology and landscape ecology of a mighty river and its basin, pp. 127-165. Dordrecht, W. Junk Publishers.

SMITH, M. A. AND D. M. GREEN. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: Are all amphibian populations metapopulations? Ecography. 28: 110–128.

SMOUSE, P. E., J. C. LONG, AND R. R. SOKAL. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Syst. Zool. 35: 627 – 632.

SOUZA, V. M., M. B. SOUZA, AND E. F. MORATO. 2008. Efeitos da sucessão florestal sobre a anurofauna (Amphibia: Anura) da Reserva Catuaba e seu entorno, Acre, Amazônia sul-ocidental. Rev. Bras. Zool. 25, 49-57.

STEBBINS, R. C. AND N. W. COHEN. 1995. A Natural History of Amphibians. Princeton University Press, New Jersey.

STEINBAUER, M., K. DOLOS, B. REINEKING, AND C. BEIERKUHNLEIN. 2012. Current measures for distance decay in similarity of species composition are influenced by study extent and grain size. Global Ecol. Biogeogr. 21, 1203-1212.

TERBORGH, J .1973. Chance, habitat and dispersal in the distribution of birds in the West Indies. Evolution. 27: 338-349.

TRENHAM, P. C. AND H. B. SHAFFER. 2005. Amphibian upland habitat use and its consequences for population viability. Ecol. Appl. 15: 1158–1168.

TUOMISTO, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography. 33: 23-45.

TUOMISTO, H., A. D. POULSEN, K. RUOKOLAINEN, R. C. MORAN, C. QUINTANA, J. CELI, AND G. CAÑAS. 2003a. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. Ecol. Appl. 13: 352-371.

TUOMISTO, H., K. RUOKOLAINEN, M. AGUILAR, AND A. SARMIENTO. 2003b. Floristic patterns along a 43-km long transect in an Amazonian rain forest. Journal of Ecol. 91: 743-756.

TUOMISTO, H., K. RUOKOLAINEN, AND M. YLI-HALLA. 2003c. Dispersal, environment, and floristic variation of western Amazonian forests. Science. 299: 241–244.

TUOMISTO, H., L. RUOKOLAINEN, AND K. RUOKOLAINEN. 2012. Modelling niche and neutral dynamics: on the ecological interpretation of variation partitioning results. Ecography. 35: 961-971.

VASCONCELOS, H. L., J. M. S. VILHENA, K. G. FACURE, AND A. L. K. M. ALBERNAZ. 2010. Patterns of ant species diversity and turnover across 2000 km of Amazonian floodplain forest. J. Biogeogr. 37: 432-440.

VON MAY, R., J. M. JACOBS, R. SANTA CRUZ, J. VALDIVIA, J. HUAMÁN, AND M. A. DONNELLY. 2010. Amphibian community structure as a function of forest type in Amazonian Peru. J. Trop. Ecol. 26: 509-519.

VONESH, J. R. 2001. Patterns of richness and abundance in a tropical African leaf-litter herpetofauna. Biotropica. 33: 502-510.

WHITTAKER, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26: 1-80.

WHITTAKER, R. J., K. J. WILLIS, AND R. FIELD. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. J. Biogeogr. 28: 453-470.

ZIMMERMAN, B. L. 1994. Audio strip transects. *In* W. R. HEYER, M. A. DONNELLY, R. W. MCDIARMID, L. A. C. HAYEK, AND M. S. FOSTER (Eds). Measuring and monitoring biological diversity: standard methods for amphibians, pp.92-97. Smithsonian Institution Press, Washington.

ZIMMERMAN, B. L. AND R. O. BIERREGAARD. 1986. Relevance of the Equilibrium Theory of Island Biogeography and Species-Area relations to Conservation with a case from Amazonia. J. Biogeogr. 13: 133-143.

ZUG, G. R., L. J. VITT, AND J. P. CALDWELL. 2001. Herpetology: an introductory biology of amphibians and reptiles. Academic Press, San Diego.

ZUQUIM, G., H. TUOMISTO, F. R. C. COSTA, J. PRADO, W. E. MAGNUSSON, T. PIMENTEL, R. BRAGA-NETO, AND F. O. G. FIGUEIREDO. 2012. Broad scale distribution of Ferns and Lycophytes along environmental gradients in Central and Northern Amazonia, Brazil. Biotropica. 44: 752-762.

Table 1. Environmental characteristics of the study sites. Means of the values extracted from BioClim (available at http://www.worldclim.org/bioclim) for the actual study plots within each area are shown.

	Amapá	Caxiuanã	Tapajós
Altitude (m)	98	30	104
Annual mean temperature (°C)	26.3	26.8	25.5
Mean temperature of driest quarter (°C)	27	27.3	26.1
Annual temperature range (°C)	10.5	11.2	12.2
Annual precipitation (mm)	2371	2223	1966
Mean precipitation of driest quarter (mm)	189	195	149

Table 2. Explanatory power of MRM with anuran species turnover (Bray-Curtis dissimilarity of log-transformed species abundances) as the dependent variable and a single distance matrix based on one environmental variable at a time as the explanatory variable. R^2 values in bold are statistically significant at $p<0.05$. Variables selected for the final multiple regression model are indicated by *, NV = the variable in question showed no variation in the area.

	Regional scale		Amapá		Caxiuanã		Tapajós	
	R^2	P	R^2	P	R^2	p	R^2	P
Day temperature	0.4%	0.19	0.2%	0.71	0%	0.91	5.7%	0.05
Night temperature	**1.5%**	**0.03**	0%	0.94	0.2%	0.73	**4.1%**	**0.04***
Day moisture	**16.9%**	**0.00***	**11.5%**	**0.00***	1.5%	0.25	**8.4%**	**0.04***
Night moisture	**10.1%**	**0.00**	**4.1%**	**0.03**	0.4%	0.65	4.5%	0.09
Canopy openness	0.8%	0.12	1.2%	0.37	1%	0.51	0.2%	0.68
Litter depth	**4.7%**	**0.00**	0.1%	0.84	0%	0.92	2.5%	0.32
Mean tree CBH	0.1%	0.62	0.1%	0.78	4.5%	0.09	6.8%	0.08
Number of tree stems	0.8%	0.09	0%	0.93	0.6%	0.54	0.1%	0.89
Watercourse width	**7.8%**	**0.00***	**22.5%**	**0.00***	2.4%	0.24	**9.6%**	**0.01**
Watercourse depth	0.1%	0.56	0.1%	0.83	0.2%	0.70	3.4%	0.35
Water velocity	0.1%	0.64	0.1%	0.74	0.9%	0.57	1.5%	0.52
Edge	**3.3%**	**0.00***	4.6%	0.07	0.8%	0.58	4.4%	0.31
Edge type	**2.8%**	**0.01***	1.2%	0.46	**3.5%**	**0.01***	NV	NV
Vegetation cover	0%	0.63	0.3%	0.52	0.1%	0.72	0.5%	0.62
Hydroperiod	**1.7%**	**0.00***	1.7%	0.06	1.5%	0.13	1.7%	0.44
Edge components	0.2%	0.07	**4.9%**	**0.02**	**2.1%**	**0.01**	0%	0.80
Edge vegetation	0.1%	0.66	NV	NV	0.6%	0.73	NV	NV
Dams	1.1%	0.08	**12.9%**	**0.01**	0.7%	0.60	0.5%	0.68
Ravine	**3.1%**	**0.01**	3.9%	0.08	NV	NV	0.4%	0.77
Riverbed type	**5.4%**	**0.00***	**5.1%**	**0.01***	NV	NV	0.4%	0.77

aquatic vegetation	0%	0.88	1.16%	0.48	0.2%	0.80	**13.1%**	**0.01***
Debris	0%	0.97	**11.7%**	**0.00**	0.1%	0.88	0.2%	0.74
Geographical distance	**30.2%**	**0.00***	**11.4%**	**0.01***	0.9%	0.13	**7.8%**	**0.04***

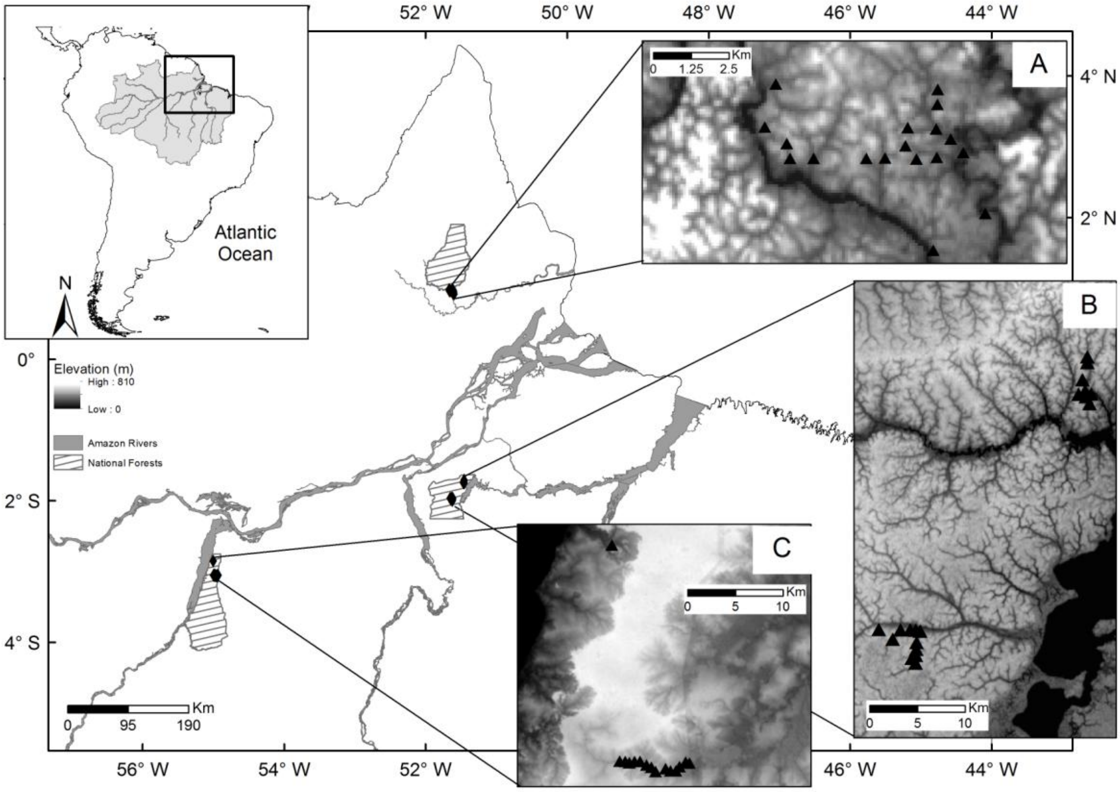
Table 3. Variation of the environmental variables on each of the areas at local scales and at regional scale. Values in bold represent variables individually selected in MRM ($p<0.05$).

	Regional scale	Amapá	Caxiuanã	Tapajós
	Mean (coefficient of variation)	Mean (coefficient of variation)	Mean (coefficient of variation)	Mean (coefficient of variation)
Day temperature (ºC)	25.6 (0.1)	26.2 (0)	25.7 (0.1)	24.7 (0.1)
Night temperature (ºC)	**24.6 (0.1)**	25.7 (0)	24.1 (0)	**23.9 (0.1)**
Day moisture (%)	**87.3 (0.1)**	**78.5 (0.1)**	90.9 (0)	**93.6 (0)**
Night moisture (%)	**88.8 (0.1)**	**82.7 (0.1)**	91.12 (0)	93.4 (0)
Canopy openness (%)	16.8 (0.3)	21.3 (0.1)	17.6 (0.2)	10.8 (0.4)
Litter depth (cm)	3.5 (0.4)	2.4 (0.5)	4.2 (0.3)	3.9 (0.3)
Mean tree CBH (mm)	22 (0.3)	25 (0.3)	20.6 (0.3)	20 (0.3)
Number of tree stems	41 (0.4)	30.7 (0.4)	46.1 (0.3)	47.4 (0.3)
Watercourse width (m)	**17.4 (1.0)**	**4.2 (1.3)**	29.5 (0.6)	**19.4 (0.7)**
Watercourse depth (cm)	39.1 (0.8)	39.5 (1.0)	30.4 (0.6)	48.3 (0.5)
Water velocity (m/s)	0.13 (1.2)	0.13 (1.0)	0.02 (2.5)	0.24 (0.8)
	Category (frequence)	Category (nº of times)	Category (nº of times)	Category (nº of times)
Margin profile	**1(22) / 2(34)**	1(4) / 2(16)	1(2) / 2(17)	1(16) / 2(1)
Margin type	**3(1) / 4(8) / 5(1) / 6(46)**	3(1) / 6(19)	**4(8) / 5(1) / 6(10)**	6(17)
Water surface covered by vegetation	1(2) / 2(19) / 3(21) / 4(14)	2(9) / 3(7) / 4(4)	2(2) / 3(8) / 4(9)	1(2) / 2(8) / 3(6) / 4(1)
Hydroperiod	**1(2) / 2(23) / 3(31)**	1(2) / 2(9) / 3(9)	2(12) / 2(7)	2(2) / 3(15)
Margin substrate	2(24) / 3(32)	**2(7) / 3(13)**	**2(9) / 3(10)**	2(8) / 3(9)
Margin vegetation	1(1) / 3(55)	3(20)	1(1) / 3(18)	3(17)
Flow obstruction	1(7) / 2(1) / 3(38) / 4(10)	1(2) / 3(10) / 4(8)	1(3) / 3(16)	1(2) / 2(1) / 3(12) / 4(2)
Ravine	**3(4) / 4(1) / 5(51)**	3(4) / 5(16)	5(19)	4(1) / 5(16)
Channel bottom type	**1(44) / 2(12)**	**1(9) / 2(11)**	1(19)	1(16) / 2(1)
Aquatic vegetation	1(51) / 3(2) / 4(3)	1(19) / 3(1)	1(17) / 3(1) / 4(1)	**1(15) / 4(2)**
Debris	1(5) / 3(3) / 4(42) / 5(6)	**3(3) / 4(13) / 5(4)**	1(1) / 4(17) / 5(1)	1(4) / 4(12) / 5(1)

FIGURE 1. Location of the study sites and the spatial distribution of the plots in (A) Amapá, (B) Caxiuanã and (C) Tapajós National Forest. Elevation range from SRTM image.

FIGURE 2. Ordination (NMDS optimized for two dimensions) of plots inventoried for frogs in Amazonian *terra-firme* rain forest in A) the entire dataset; B Amapá; C) Caxiuanã, and D) Tapajós. Dissimilarities between plots based on Bray-Curtis index calculated with log-transformed species abundances. Crosses (+) represents species ordination. Arrowhead coordinates indicate Pearson correlation coefficients between original environmental variables and each NMDS axis using "envifit" r function (only significant correlations are shown). DT= Day temperature, NT= Night temperature, DM= day moisture, NM= night moisture, CC= canopy openness, LD= Litter depth, Tr= Number of tree stems, WW= Water width, WV= Water velocity, MP= Margin profile, Hp= Hydroperiod, Ra= Ravine, WC= Channel bottom type, MT= Margin type, MSV= Water surface covered by vegetation, FO= Flow obstruction, Db= Debris, AV= Aquatic vegetation.

FIGURE 3. Venn diagram representing the partitioning of the variance in anuran species turnover between plots into fractions explained by environmental differences and geographical distances in the entire dataset (regional scale; A) and in each of the study areas separately (local scale): Amapá (B), Caxiuanã (C) and Tapajós (D). R^2 values (in %) obtained from MRM are given for each fraction.


52° W
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44° W
4° N
2° N
0°
2° S
4° S
56° W
54° W
52° W
46° W
44° W
Atlantic Ocean
N
Elevation (m)
High : 810
Low : 0
Amazon Rivers
National Forests
Km
0 95 190
A
Km
0 1.25 2.5
B
Km
0 5 10
C
Km
0 5 10

Figure 1

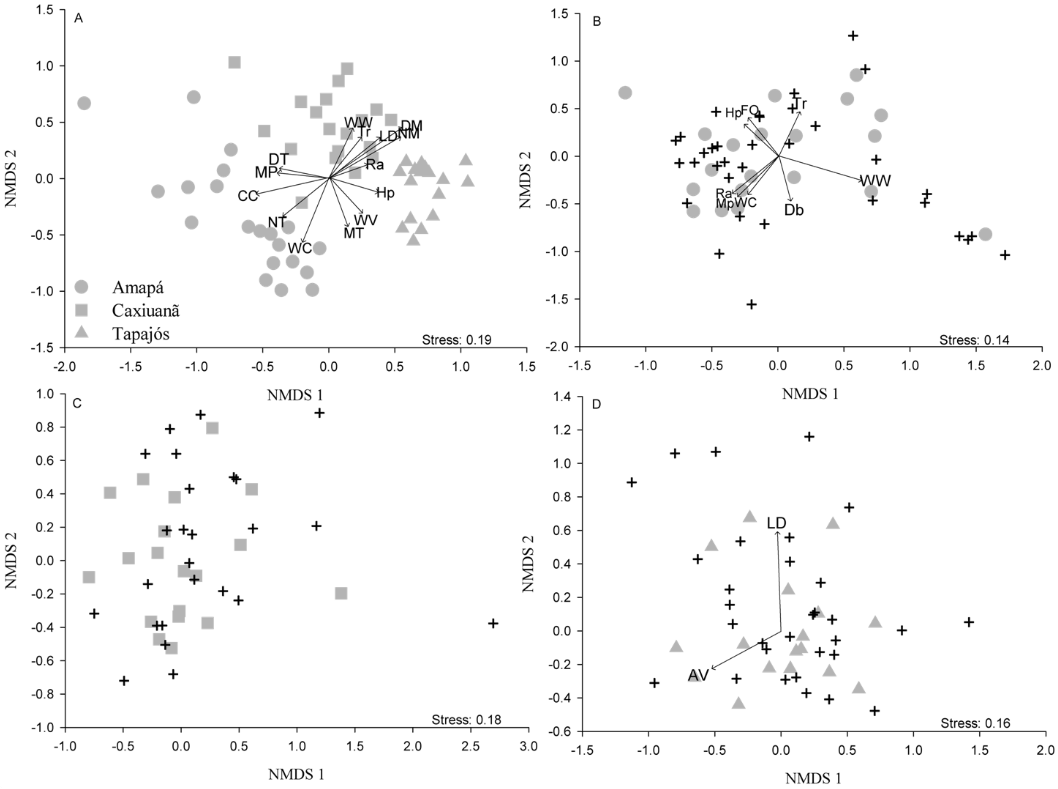
A
NMDS 2
NMDS 1
WW
Tr
DM
LD
NM
Ra
DT
MP
CC
Hp
NT
WV
MT
WC
Amapá
Caxiuanã
Tapajós
Stress: 0.19
B
Hp
FO
Tr
WW
Ra
Mp
WC
Db
Stress: 0.14
C
Stress: 0.18
D
LD
AV
Stress: 0.16

Figure 2

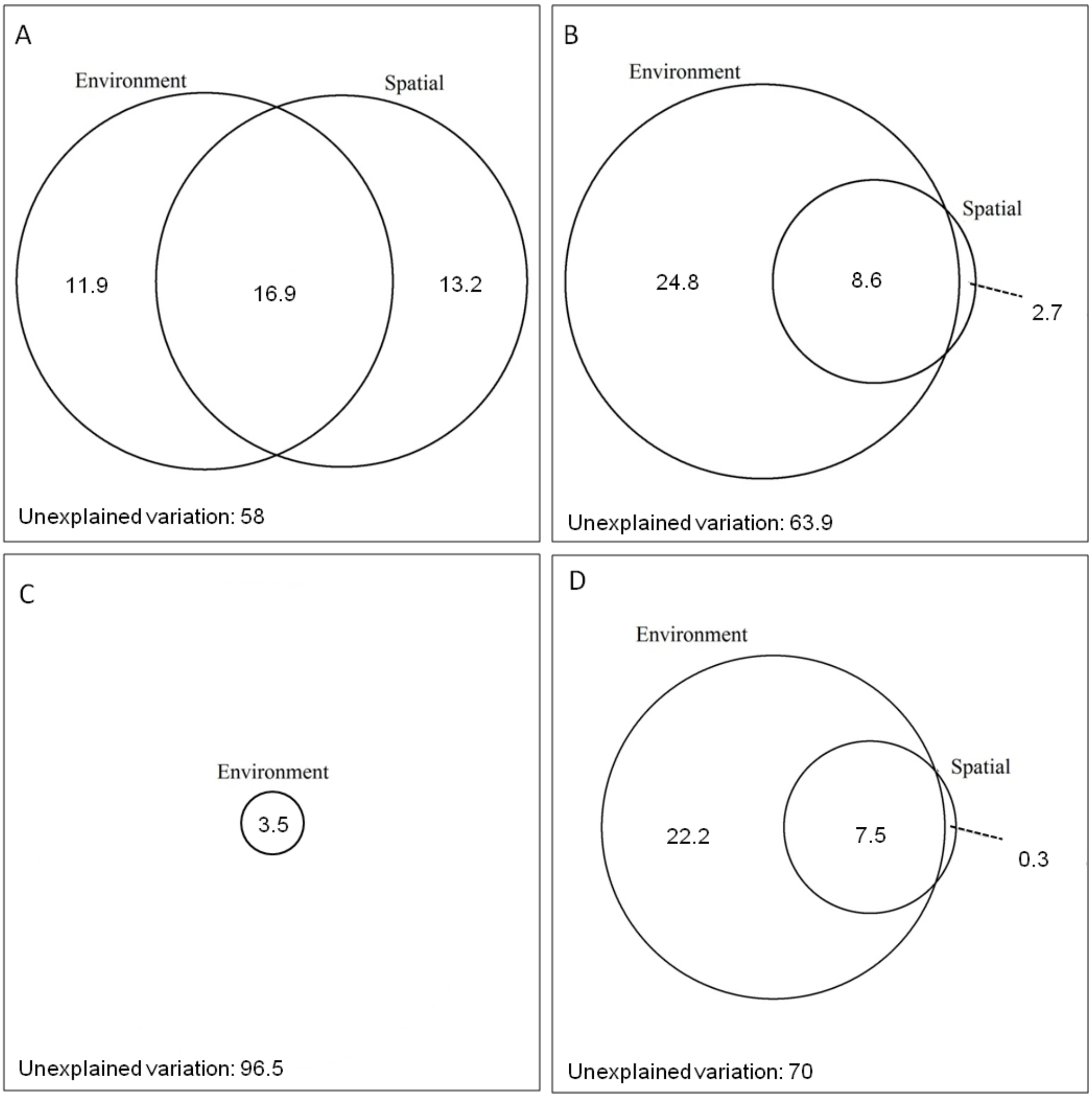
A
Environment
Spatial
11.9
16.9
13.2
Unexplained variation: 58
B
Environment
Spatial
24.8
8.6
2.7
Unexplained variation: 63.9
C
Environment
3.5
Unexplained variation: 96.5
D
Environment
Spatial
22.2
7.5
0.3
Unexplained variation: 70

Figure 3

Appendix SI

Only one option to each variable was chosen for each watercourse physical characteristic.

Physical characteristics	Transformation	Condition	Score
Margin profile	Gower	Sloping	1
		Flat	2
Margin types	Euclidian	dry bare soil	1
		dry soil with and without vegetation	2
		the previous two, plus wet bare soil	3
		the previous three, plus moist soil with and without vegetation	4
		the previous four, plus flooded soil without vegetation	5
		the previous five, plus flooded soil with and without vegetation	6
Water surface covered by vegetation	Euclidian	0%	1
		25%	2
		50%	3
		75%	4
		100%	5
Hydroperiod	Gower	short-term temporary (rain puddles, lasting up one week)	1
		long-term temporary (entire rainy season)	2
		Permanent (lentic or lotic water: streams, lakes, ponds, flooded fields, etc.)	3
Margin substrate	Gower	dry soil	1
		moist soil	2
		wet soil, with small ponds	3
Margin vegetation	Gower	grass and a few shrubs	1
		grass, with some pioneer trees and shrubs	2
		mixed pioneer trees with mature trees	3
		more than 90% of non-pioneer plants	4
Flow obstruction	Euclidian	free channel, few objects moving with the flow	1
		many objects moving with the flow	2
		rocks and logs, filled with sediment	3
		rocks and driftwood stable	4
Ravine	Gower	Unstable	1
		free soil, spaced layers of grass and shrub	2
		stable, but not sustained for grasses or shrubs	3
		stable, sustained for rocks, grasses, roots or shrubs	4
		no ravine	5
Water channel	Euclidian	uniform channel silt and sand free, no stones	1
		silt channel, gravel and sand in stable places	2
		easily movable stones, with little silt	3
		stones of different sizes	4
Aquatic vegetation	Euclidian	tangly of algae, vascular plants dominate the channel	1
		tangly of algae, few vascular plants and mosses	2

		dominant algae, aquatic or semi-aquatic vascular plants on the banks	3
		when present consists of patches of moss and algae	4
Debris	Euclidian	fine sediment anaerobic, no gross debris	1
		no leaves or wood, gross and fine organic material, sediment	2
		little leaf and wood, fine organic debris without sediment	3
		leaves and woody material sediment	4
		leaves and woody material without sediment	5

Appendix S2

Amphibian species recorded by site and by reproductive environment.

TAXA	Amapá National Forest	Caxiuanã National Forest	Tapajós National Forest	lentic water	lotic water	direct development (parent's back)	on ground/ lentic water	direct development (on the ground)	on leaves of trees above the water/ lentic water	on leaves of trees above the water/ lotic water	water in tree holes or aerial plants	foam nest on ground/ lentic water	Chamber on ground/ lentic water	foam nest on pond	foam nest on ground
Allophrynidae															
Allophryne ruthveni	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Aromobatidae															
Allobates femoralis	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Allobates gr. *trilineatus*	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Allobates gr. *trilineatus* sp2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Bufonidae															
Amazophrynella bokermanni	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Amazophrynella minuta	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Atelopus hogmooedi	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Rhaebo guttatus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Rhinella castaneotica	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Rhinella lescurei	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Rhinella marina	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Centrolenidae				0	0	0	0	0	0	0	0	0	0	0	0
Hyalinobatrachium mondolfii	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Hyalinobatrachium fleischmanni	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Hyalinobatrachium sp.	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Vitreorana oyapiensis	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Ceratophryidae															
Ceratoprhys cornuta	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Craugastoridae															
Pristimantis chiastonotus	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pristimantis fenestratus	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Pristimantis marmoratus	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dendrobatidae															
Adelphobates castaneoticus	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Ameerega pulchripecta	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
*Ranitomeya ventrimaculata**	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Hylidae															
Dendropsophus brevifrons	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Dendropsophus minimus	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Dendropsophus minusculus	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0

Dendropsophus sp nov	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dendropsophus sp2 nov	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Hypsiboas boans	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Hypsiboas calcaratus	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Hypsiboas cinerascens	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Hypsiboas dentei	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hypsiboas geographicus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Hypsiboas leucocheilus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Hypsiboas ornatissimus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hypsiboas wavrini	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Osteocephalus inframaculatus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Osteocephalus leprieurii	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Osteocephalus oophagus	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Osteocephalus taurinus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
*Phyllomedusa bicolor***	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
*Phyllomedusa vaillantii***	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0
Scinax boesemani	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Scinax cf. cruentommus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Scinax garbei	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Scinax nebulosus	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Scinax sp nov	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Scinax cf. x-signatus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Trachycephalus coriaceus	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Trachycephalus hadroceps	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Trachycephalus resinifictrix	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Leiuperidae				0	0	0	0	0	0	0	0	0	0	0	0
Engystomops freibergi	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Leptodactylidae															
Adenomera andreae	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Leptodactylus knudseni	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Leptodactylus leptodactyloides	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Leptodactylus mystaceus	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Leptodactylus paraensis	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
Leptodactylus pentadactylus	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Leptodactylus petersii	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Leptodactylus rhodomystax	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Leptodactylus stenodema	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Microhylidae															
Chiasmocleis hudsoni	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Chiasmocleis sp nov	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Chiasmocleis shudikarensis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hamptophryne boliviana	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pipidae															
Pipa pipa	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Total richness	40	26	32	26	1	1	8	3	8	4	4	4	2	3	1

Richness of unique species	21	4	12	-	-	-	-	-	-	-	-	-	-	-	-

* tadpoles are carried to the water in bromeliads

** build nests on leaves

Capítulo 3

How differences in anuran reproductive modes can affect their turnover: comparing scales and habitats

Bitar, Y.O.C., Tuomisto, H., Pinheiro, L.P.C. & Santos-Costa, M.C.

How differences in anuran reproductive modes can affect their turnover: comparing scales and habitats

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ABSTRACT

Variation partitioning of species turnover is a common approach to understanding how communities change along environmental gradients or geographical distances. Understanding the factors that affect species turnover is a prerequisite for understanding community assembly and function. When species turnover is related to environmental gradients, it is intimately linked to species responses along those gradients. However, such analyses only give information on general community patterns, not any information on how many species are actually reacting to the environmental gradients of interest, or what kinds of responses there are. This kind of information can be obtained from the so called Huisman, Olff, Fresco (HOF) models. In the present paper, we combine both approaches to test Amazonian frogs turnover among distinct scales (Amazonian, regional and local), habitats (*terra firme* x *várzea*) and species differing in reproductive modes (aquatic, vegetation and terrestrial breeders). We sampled 56 plots distributed in three *terra firme* forest sites, and 40 plots in two

sites of *várzea* forest environment. We found aquatic breeders as dominants in all areas, but a higher proportion in *várzea* environment, while a *terra firme* site with flooding regime (Caxiuanã) presented the higher proportion of species laying eggs on the vegetation, and terrestrial breeders were more common in the other two sites. Despite that difference, those two environments did not differ regarding environmental heterogeneity. Also, large differences in turnover partitioning among scales were detected, with geographical distance having greater importance in Amazonian than regional or local scale. The opposite was observed with the environmental component, that were more important in fine scales. Dividing the total species table according to their reproductive mode did not increased turnover explanation power, but each group proved to respond to different factors. Our HOF analyzes showed strong congruencies with the observed turnover patterns, but the same variables presented distinct importance to species according to the area tested. However, tropical forests without a clear gradient make difficult to choose a single variable that most influence species turnover, and a different set of many variables acting together on each area seems to act as drivers of species turnover.

INTRODUCTION

Understanding the factors that affect species turnover is a prerequisite for understanding community assembly and function. When species turnover is related to environmental gradients, it is intimately linked to species responses along those gradients (Nekola & White 1999, Buckley & Jetz 2008). If species have narrow ranges along a given environmental gradient, high species turnover among communities along that gradient can be expected.

Many studies have approached the question of community assembly by partitioning the variation in site-to-site species turnover to components uniquely and jointly explained by alternative explanatory factors. Typically, variation explained by environmental differences is interpreted in terms of niche processes and variation explained by geographical distances is interpreted in terms of dispersal processes (Tuomisto *et al.* 2003; Lichstein 2007; Qian 2009; Qian & Ricklefs 2012; Bitar *et al.* Chapter 2). Due to their limited dispersal abilities, amphibians are known to respond quickly to spatial changes in environmental characteristics (Arita & Rodriguez 2002).

This group also presents a high sensitivity to habitat conditions (Feder & Burggren 1992), and compositional dissimilarities may be a reflection of environmental variability. In Amazonian communities, frog turnover was previously related to variation in some important factors. Areas with higher trees density showed higher richness of anurans with terrestrial reproduction, and depending on the species, topographic and edaphic factors, such as slope and clay content, may increase or decrease those species abundance (Menin *et al.* 2007). Also, the presence of water seems to be the one of the most important characteristics to anurans (Zimmerman & Bierregard 1986), with sites near to streams (riparians) harboring more and different species than the non-riparian sites (Menin *et al.* 2011, Ribeiro *et al.* 2012). The anthropogenic component is also showed important to frogs. Heavily impacted habitats show a distinct community composition, with reproduction more adapted to dehydration and with lower turnover when compared to forested habitats (Bitar *et al.* 2012, 2014).

However, such analyses only give information on general community patterns, and similar results may be obtained for a variety of reasons. For example, the lengths of the observed environmental gradients and the absolute amounts of species turnover have a strong influence on the results. A given environmental variable may have low explanatory power in the analyses because it is truly irrelevant for the organisms of interest, but also because in this particular dataset it did not vary enough for any effects to be detectable, or because the observed gradient was so long that the saturation of compositional dissimilarities became a problem (Tuomisto *et al.* 2012). Assessing the behavior of the individual species along a gradient may help to separate between these alternatives. For example, what proportion of the species is actually reacting to the environmental gradients of interest, and what kinds of responses do they show?

Species responses along environmental gradients are generally thought to be unimodal (Austin 1985, Rydgren *et al.* 2003): highest abundance is attained at species-specific optimum conditions, and abundance decreases towards both extremes of the environmental gradient (Huisman *et al.* 1993). If only a part of the gradient is sampled, species responses will be truncated and may be observed as linear or leveling off. Species response shapes can be identified using the HOF model approach (Huisman *et al.* 1993; Oksanen & Minchin 2002, Jansen & Oksanen 2013). Also, the slope and shape of response curves along environmental gradients are employed to quantify species turnover (Oksanen & Tonteri 1995, Peppler-Lisbach & Kleyer 2009, Peper *et al.* 2011), and identify how species in a community are responding to the environmental variables would help to elucidate species turnover pattern in an area. Analyze species probabilities of occurrence along a gradient allow us to infer about the optimum range of the species (Jansen & Oksanen 2013), and more easily discuss observed turnover results.

Habitat properties that are thought to influence anuran distributions include air moisture and temperature (Crump 1971, Vonesh 2001, Haddad & Prado 2005), water availability (Zimmerman & Bierregaard 1986), canopy cover and pond morphology (Provete *et al.* 2014), vegetation structure (Crump 1971, Halverson *et al.* 2003, Souza *et al.* 2008) and volume and depth of leaf litter (Giaretta *et al.* 1999). To our knowledge, there have been no direct assessments on anuran species response shapes along these gradients in Amazonia. Few studies have analyzed species probability of occurrence along environmental gradients, and most of them with plants in non tropical habitats (Rydgren *et al.* 2003; Murphy *et al.* 2010; Harris *et al.* 2011). Studying plants along grazing gradients, most of the species showed higher probability of occurrence in areas with low grazing effect and only a few species were promoted by moderate grazing, resulting in high turnover rate along it (Peper *et al.* 2011). Furthermore, those authors also suggest that species which tolerate or occur in a very small part of the total gradient length, grazing intensity in that case, would probably increase the turnover to some extent in this gradient (Peper *et al.* 2011).

Many of the environmental variables that have been found important for anurans are related to properties of the reproductive habitat (Haddad & Prado 2005, Bitar *et al.* 2012; Silva *et al.* 2012). Therefore, it can be expected that anurans with distinct reproductive modes (e.g. aquatic or terrestrial ovipositors) may respond to different environmental factors (Landeiro *et al.* 2014). Analyzing a single community in Central Amazonia, Landeiro *et al.* (2014) concluded that aquatic breeding species are more susceptible to variation in environmental variables, whereas terrestrial species are more clearly spatially autocorrelated. They also found that distance to the nearest stream was the best predictor of the species richness and abundance of aquatic breeding frogs, with an increase in distance resulting in a decrease in the numbers of species and individuals (Menin *et al.* 2011). In contrast, the majority of terrestrially breeding anuran species were influenced by topographic and edaphic variables, such as slope, soil clay content and pH (Menin *et al.* 2007). This indicates that differences in anuran community structure related to breeding habitat could lead to different community-level responses to environmental variables among localities. Earlier studies aiming to identify the main drivers of tropical anurans turnover have reached different conclusions (Ernst & Rödel 2008, Keller *et al.* 2009, Bitar *et al.* chapter 2), but did not address the reproductive component in their analysis.

Correlations among anuran turnover, environmental characteristics and species reproductive modes remains poorly understood in a general framework. There is a consensus that differences in habitat types result in distinct community composition (Von May *et al.* 2010), what may lead to a different subset of reproductive modes among those communities (Bitar *et al.* 2012). The Amazon forest is a region with high ecological heterogeneity and floristic differences among sites (Tuomisto & Ruokolainen 1997). Therefore, two broadly defined and widespread forest categories in Amazonia are the non-flooded forests (*terra firme*) and the forests that are seasonally flooded by white-water rivers (*várzea*). So, it is expected that anurans environmental relationships are different in *terra firme* and *várzea* forests, linked to differences in ecological characteristics presented in each one, and that these relationships may also differ by reproductive mode. Considering that different habitat types tend to present their own community specialized on that local ecological characteristics (Bitar *et al.* 2012), studies comparing different habitat types would show a wider perspective on the regional aspect of the species turnover.

Here, we combine two analytical approaches to understand how the patterns of amphibian species turnover are related to environmental factors in Amazonian *terra firme* and *várzea* forests. Firstly, we carry out variation partitioning analyses to clarify which environmental variables can be considered important for the species turnover of frogs in our study areas and to compare their importance to that of geographical distance. Then, we look into those communities in more detail to document the response shapes of the individual species. We then present statistics about the commonness of the different response shapes in different geographical regions, for multiple environmental variables, and for anurans of distinct breeding habitats (aquatic, vegetation and terrestrial eggs). Finally, we relate the relative commonness of the different reproductive modes in multiple geographical areas to the observed environmental gradients.

MATERIAL AND METHODS

Study area

Terra firme forests: Three areas are grouped in this classification, Amapá (1°2'32"S and 51°56'32" W), Caxiuanã (1°47'32.3"S and 51°26'02.5"W) and Tapajós (03°04'00"S and 54°54'00"W) (Figure 1A, B and C, respectively). They are located in the eastern part of the Brazilian Amazon, within protected areas. Some classifications use to estimate around 65% of the total seven million square kilometers that make up the Amazon basin consist in *terra firme* forest (Oliveira & Amaral 2004), but it probably are not distinguishing them from the floodplains of the streams, named riparian forest (Junk *et al.* 2011). *Terra firme* forest develops in areas not liable to floods because they are located in a higher region of the Amazon relief. A total of 56 plots were used for this category, distributed as 20 in Amapá, 19 in Caxiuanã and 17 in Tapajós (see chapter 2 for more details).

Várzea forests: Wetland areas, that include *Várzea* forest, correspond to 30% of the Amazon forest (Junk *et al.* 2011) and only *Várzea* forest are estimate to cover an area of more than 400,000 km^2 (Melack & Hess 2010). We sampled two areas in this environment, Mamirauá (01º49'00"S and 65º42'00"W) and Amanã (01º54'00"S and 64º22'00"W) (Figure 1D and E, respectively). On each area 20 plots were established, totalizing 40 plots in *várzea* forests that are characterized by average amplitude of flooding about 10 m, corresponding to a submersion of trees of up to 230 days per year (Junk 1989). In this area, plots were established in order to have at least half them with non-flooded soil, to allow both terrestrial and aquatic reproductive species to occur.

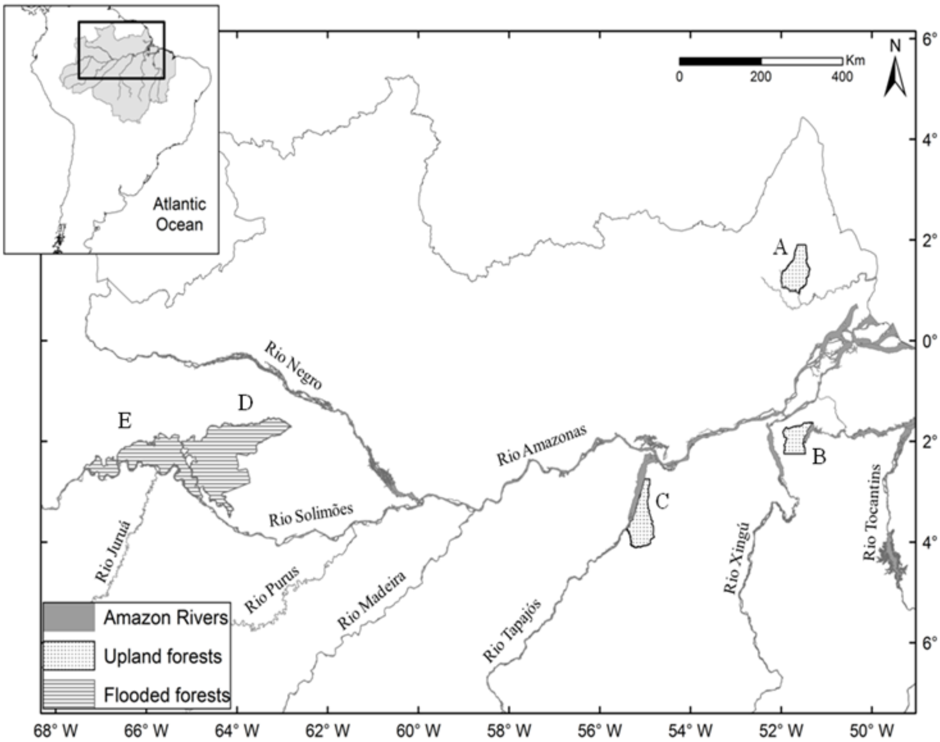


Figura 1. Site locations in Amazonian *terra firme*: National Forest (NF) ofAmapá (A), NF Caxiuanã (B), NF Tapajós (C); and Sustainable Development Reserves (SDR) of *várzea* forests: SDR Amanã (D) and SDR Mamirauá (E).

Survey methods

Fieldwork was done during the same rainy season in all three sites in *terra-firme* forests, between January and April 2011, and expeditions lasted 26 days on average. In *várzea* forests all 40 plots were sampled in March 2012. Each sampling unit (plot) was 2100m² in size (70m x 30m) and separated by a distance of at least 500 m from the nearest other plot. Plot boundaries were marked with a string, and the surveys were performed using visual sampling (visual encounter surveys) and auditory survey, simultaneously (Crump & Scott 1994, Zimmerman 1994, Menin *et al.* 2007). Searches were conducted twice in each plot (Zimmerman 1994, Crump & Scott 1994), once during the day (between 14:00h and 18:00h) and once during the night (between 20:00h and 24:00h).

All plots contain at least one pond/stream covering maximum half of the plot, in order to control the effect of the presence of water in the plots and maximize the collection effort, since the presence of water is considered one of the most important factors for anurans (Zimmerman & Bierregard 1986) and their absence in some plots could result in bias or misinterpretation of results. During each period, three collectors walked side by side for at least 2 hr, or until no new frog individuals were recorded. All frog individuals that were either sighted or heard calling inside the plot were identified to species and counted. All possible individuals were captured to avoid recounting of the same specimen and to facilitate the counting. At least one individual of each species was preserved as a voucher specimen for later confirmation of the species identification and to standardize the morphospecies classification among all areas when identification to names species was not possible due to taxonomical uncertainties. Specimens collected were preserved in alcoholic solution at 70%, and will be deposited in the herpetological collection of the *Museu Paraense Emílio Goeldi* in the end of the project (temporarily deposited in zoological collection of Universidade Federal do Pará). The individuals that were not needed as vouchers were released as soon as the observation period ended.

Reprocductive modes

Reproductive modes were observed in the field for many of the species, and the IUCN (2014) website was used to complement the information. Species were divided into three categories according to where they deposit their eggs (Appendix 1):

1) Aquatic: eggs laid directly into the water, where the tadpoles develop;

2) Aquatic vegetation: eggs laid on plants above the water, tadpoles drop into the water and develop there;

3) Terrestrial: terrestrial eggs and tadpoles, or terrestrial eggs on the ground with direct development (egg hatch with young adult morphology) (e.g. *Pristimantis* genus)

Three species (*Osteocephalus oophagus*, *Trachycephalus coriaceus* and *T. hadroceps*) were considered terrestrial breeders in spite of their aquatic eggs. These species use accumulated rain water in tree cavities to reproduce, and are not expected to respond to properties of the ponds that were measured in this study.

Environmental variables

In each plot, we measured 22 environmental variables. These are explained in detail in Bitar et al. *not published* (Chapter 2). Eleven of the environmental variables specifically describe the environment of the watercourses and their surrounding area: margin profile (MP), margin type (MT), water surface covered by vegetation (VC), hydroperiod (Hy), margin substrate (MS), margin vegetation (MV), flow obstruction forming dams (FO - presence and kind of material obstructing water flow), ravine (Ra), water channel (WC - kind of material present on the bottom of the watercourse channel), aquatic vegetation (AV) and debris (De). A single observer (always the same) covered the approximate distance of 30m along the watercourse and filled a descriptive protocol taking into account what was observed in this stretch. A protocol was filled only once for each plot.

In addition, we also measured another eleven variables: day temperature (ºC), night temperature (ºC), day moisture (%), night moisture (%), canopy openness (%), litter depth (cm), watercourse width (mm), watercourse depth (mm), water velocity (m/s), mean CBH (tree circumference at breast height - mm) and number of tree stems. Two temperature and moisture measurements were taken in each plot, once during the day survey and once during the night survey. Canopy openness (%) is based on the average of four photos per plot taken with a digital camera attached to a tripod 50cm above the ground. The photographs were analyzed with the program ENVI 4.5 (ITT Visual Information Solutions, Boulder, Colorado, USA). Litter depth was measured at four points within each plot. Usually there was one measurement point in each corner, but if the spot was affected by a waterbody, the measurement was taken from the middle of the plot. The average of the four values was used in the analyses. Water velocity was measured during the day survey, by timing how many seconds a piece of Styrofoam needed to travel one meter in the fastest point of the watercourse. Width and depth measurements were taken with a tape measure at the widest or deepest point of the watercourse, respectively. Number of tree stems and mean CBH were measured in two sub-plots (5m x 10m) located at opposite corners within the plot. All woody plants with CBH ≥ 5cm inside the sub-plots were taken into account.

Statistical analysis

Species turnover was calculated between all possible pairs of plots using the Bray-Curtis dissimilarity index. Species abundances were natural log-transformed (log (x)+1) before calculating the dissimilarities. All analyses were then carried out both at the local scale (dissimilarity matrices constructed for each of the five areas separately) and at the regional scale (all plots from all five areas combined into one dissimilarity matrix).

Environmental dissimilarity matrices were calculated separately for each environmental variable. Euclidean distance was used for the quantitative variables and Gower distance for the categorical ones (see previous chapter for details with environmental tables). Geographical distance was calculated from plot latitude and longitude using Euclidean distance. To account to differences in the proportion of species on each reproductive mode, we performed a table with the number of species on each reproductive category by sampling unit, in order to have the proportion of species with aquatic, aquatic vegetation or terrestrial eggs. Ternary plots were created using ggtern package on R.

To check if the turnover of species with similar reproductive mode are responding to the same variables in the different areas, we performed multiple regression on distance matrices (MRM; Manly 1986, Smouse *et al.* 1986, Legendre *et al.* 1994, Legendre & Legendre 1998, Tuomisto *et al.* 2003c, Lichstein 2007). First we used all species together as a single community, then we performed the same analyses for species that have some level of reproductive dependence with water bodies (aquatic + aquatic vegetation species), and then separately only with species with aquatic eggs, with species with eggs on the vegetation above the water (aquatic vegetation) and for species with terrestrial reproduction. This approach was used for all species (amazonian scale), for species collected in all *terra firme* and then in *várzea* forests (regional scale), and for each of the five areas individually (local scale). To assess the relative contributions of geographical distances and the 22 environmental dissimilarity matrices to explaining species turnover, we first made an initial selection of the explanatory variables by running the regression analyses with each dissimilarity matrix separately. Those environmental variables that were found significant on their own were used to build an initial MRM model, which was then simplified using backward elimination until the final MRM model (MRM_{env}) contained only those explanatory variables that made a significant ($p<0.05$) partial contribution to explaining species turnover. If the model with just the geographical distance matrix (MRM_{geo}) was significant, an additional MRM containing all variables from both MRM_{env} and MRM_{geo} was run (MRM_{all}).

Differences on environmental heterogeneity between *várzea* and *terra firme* forests were tested by the average distance to median (Anderson 2006) based on the 22 environmental variables measured. The mixed-variables coefficient of distance generalizes Gower's general coefficient (Pavoine *et al.* 2009) was used to calculate the distance matrices used on the function betadisper. Statistical differences between groups were tested by 10000 permutations.

The species probability of occurrence along the continuous variables were calculated based on the Huisman-Olff-Fresco (HOF) models (Huisman *et al.* 1993). For detecting the shape of species responses along those gradients, we considered all seven shapes proposed by Jansen & Oksanen (2013) which extended the initial five unimodal shapes including two bimodal shape possibilities (Figure 2). Models were calculated separately for each study area, and the best model selected was the most common after 1000 permutations. Only species occurring in at least five plots were included in these analyses. HOF models were calculated using the HOF function implemented in eHOF package (Jansen & Oksanen 2013).

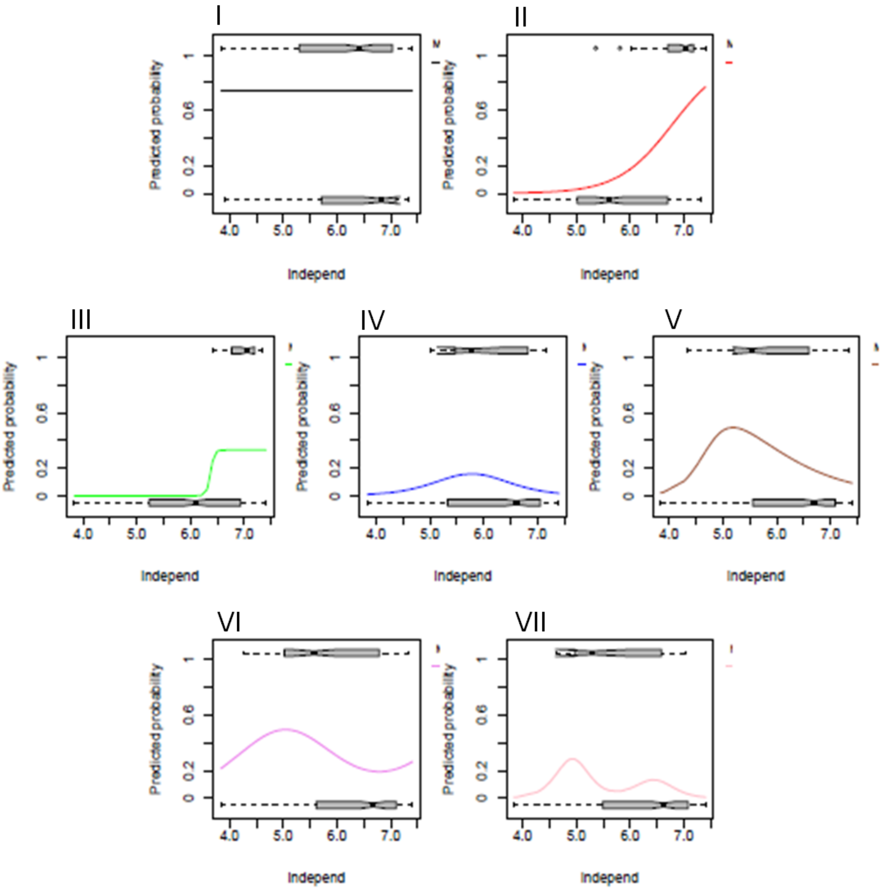


Figure 2. Examples of HOF models I to VII along a pH gradient with plotted shape parameter values. Grey boxes in the upper part correspond to central and outer niches (modified from Jansen *et al.* 2015).

RESULTS

Species reproductive modes and habitat heterogeneity

We registered a total of 92 species in the five study areas: 40 in Amapá, 26 in Caxiuanã, 32 in Tapajós, 30 in Mamirauá and 26 in Amanã. Most species had aquatic reproduction in terra firme (36/65 species) and even more so in varzea (26/37). The next most common reproductive mode was terrestrial (16/65 in terra firme and 6/37 in varzea) and finally aquatic vegetation (13/65 in *terra firme* and 5/37 in *várzea*). The two forest types differed significantly in the proportions of species on each reproductive category (figure 3).

The aquatic reproductive mode was the most common mode in Amanã and Mamirauá, while reproduction in vegetation above the water had greater importance in Caxiuanã. A more homogeneous distribution of species among the reproductive categories was found in Amapá and Tapajós, with more species reproducing out of the water in comparison to the other sites (figure 3).

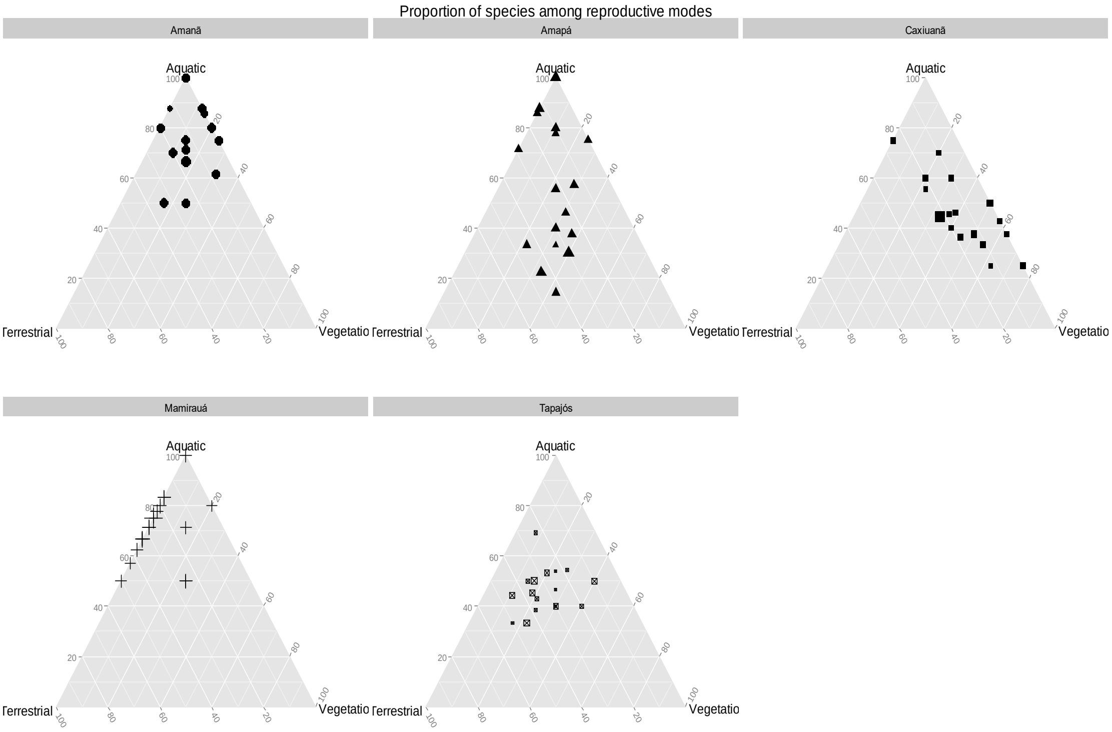


Figure 3. Proportion of aquatic, vegetation and terrestrial species on each area. Plot size according to environmental variable Canopy openness in that plot (• 10%, • 20%, ● 30%, ● 40%). Areas: Amanã(●); Amapá (▲); Caxiuanã (■); Mamiruá (+) and Tapajós (⊠)

The environmental characteristics of *várzea* and *terra firme* forests were clearly different (Figure 4), but no significant differences in environmental heterogeneity between the two forest categories could be observed (p=0.64, average distance to median TF=0.249, VA=0.248).

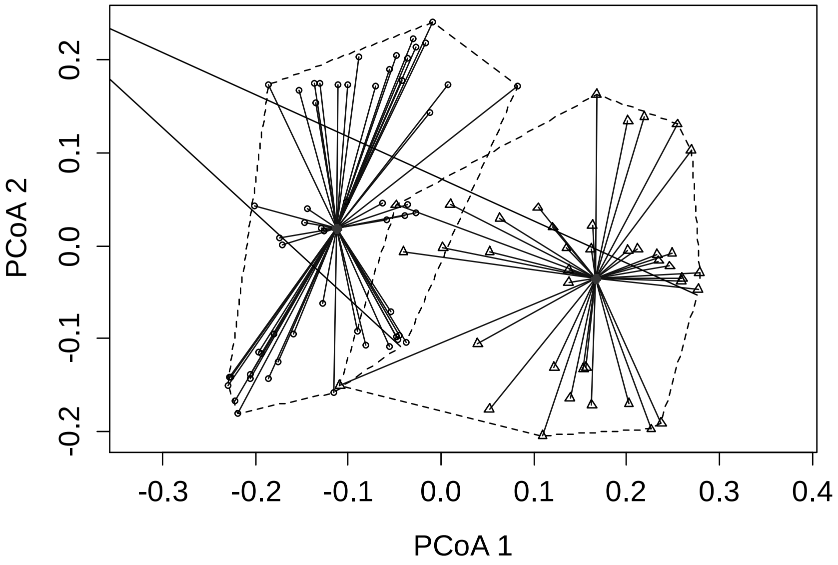


Figure 4. Average distance to median based on environmental characteristics in Amazonia, Brazil. Dots are *várzea* and triangles *terra firme* forests. Lines represent distance to median on each group.

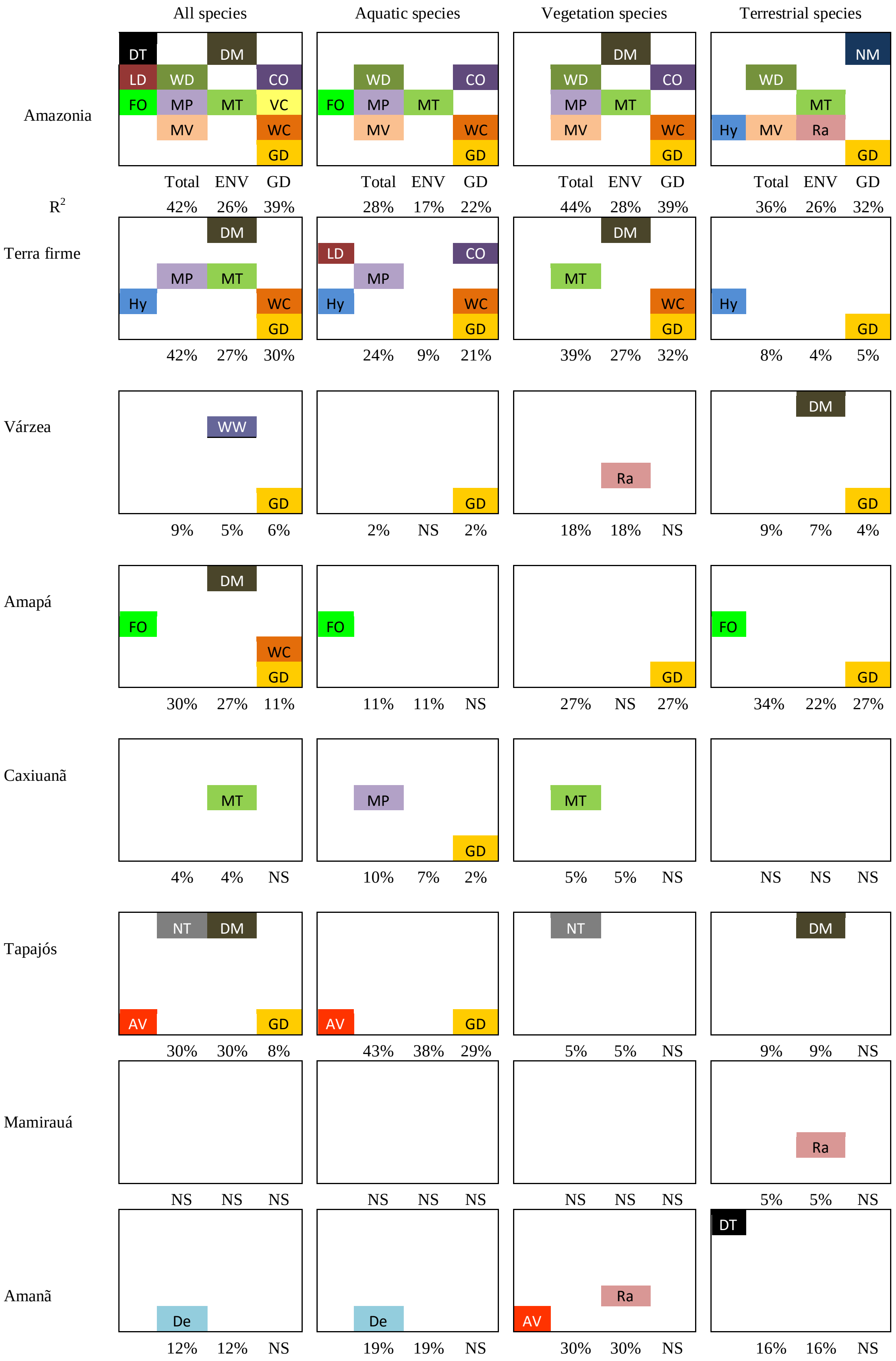
Environmental and geographical processes

In the MRM analyses carried out at the broadest extent (all five areas together), 42.3% of the variation in frog species turnover could be explained by variation in environmental and spatial distances. When MRM analyses were done using species of each reproductive mode separately, the proportion of variation that could be explained was generally smaller (aquatic + vegetation species jointly = 38.5%, only aquatic = 27.5% and terrestrial = 36%), but slightly higher in one case (only vegetation = 44.3%). The spatial component was the most important at this scale, independent of the anuran group used (ranging from 22.1 to 38.9%). At the same time, more environmental variables were selected as important at at this scale (extent) than at the more local scale (Table 1). Those that appeared most often were air moisture (day or night), canopy openness, margin profile, margin type, margin vegetation and water channel.

At the regional extent, much more turnover was explained in *terra firme* (ranging from 8.3% to 42.3% for the different frog groups) than in *várzea* forests (2.2% to 17.7%). Both environmental and spatial components were significant in *terra firme*, independent of the species group. In *várzea* forests, the environmental differences were non-significant for aquatic and vegetation species analyzed together and aquatic species alone. Moreover, the geographical component was non-significant for species with vegetation reproduction (Table 1).

At the local scale, the results differed among sites. Species turnover in Mamirauá showed no correlation with either environmental or spatial factors. In Amanã, 12% of the variation was explained by environmental variation (specifically variation in Debris characteristics) but geographical distance was non-significant (Table 1). Of the *terra firme* sites, Amapá and Tapajós gave similar results, with around 30% of the variation in species turnover explained by measured environmental variables and much higher proportion related to variation in environmental factors. On the other hand, Caxiuanã was more similar to the *várzea* sites, with only 4% of the variation in turnover explainable with variation in environmental factors (Table 1).

Table 1. Variables retained in the final model and explanatory power (R^2) of environmental and geographical distances when explaining variation in frog species turnover. Separate analyses were carried out for all species together and each reproductive mode separately. **AV**: Aquatic vegetation; **CO**: Canopy openness; **De**: Debris; **DM**: Day moisture; **DT**: Day temperature; **FO**: Flow obstruction; **GD**: Geographic distance; **Hy**: Hydroperiod; **LD**: Leaf litter depth; **MP**: Margin profile; **MT**: Margin type; **MV**: Margin vegetation; **NM**: Night Moisture; **NS**: Not significant; **NT**: Night temperature; **Ra**: Ravine; **VC**: Water surface cover; **WC**: Water cannel; **WD**: Water depth; **WW**: Water width. NS= Not significant; GD= geographical distance.


All species
Aquatic species
Vegetation species
Terrestrial species
Amazonia
DT
DM
LD
WD
CO
FO
MP
MT
VC
MV
WC
GD
WD
CO
FO
MP
MT
MV
WC
GD
DM
WD
CO
MP
MT
MV
WC
GD
NM
WD
MT
Hy
MV
Ra
GD
Total ENV GD
R2
42% 26% 39%
Total ENV GD
28% 17% 22%
Total ENV GD
44% 28% 39%
Total ENV GD
36% 26% 32%
Terra firme
DM
MP
MT
Hy
WC
GD
42% 27% 30%
LD
CO
MP
Hy
WC
GD
24% 9% 21%
DM
MT
WC
GD
39% 27% 32%
Hy
GD
8% 4% 5%
Várzea
WW
GD
9% 5% 6%
GD
2% NS 2%
Ra
18% 18% NS
DM
GD
9% 7% 4%
Amapá
DM
FO
WC
GD
30% 27% 11%
FO
11% 11% NS
GD
27% NS 27%
FO
GD
34% 22% 27%
Caxiuanã
MT
4% 4% NS
MP
GD
10% 7% 2%
MT
5% 5% NS
NS NS NS
Tapajós
NT
DM
AV
GD
30% 30% 8%
AV
GD
43% 38% 29%
NT
5% 5% NS
DM
9% 9% NS
Mamirauá
NS NS NS
NS NS NS
NS NS NS
Ra
5% 5% NS
Amanã
De
12% 12% NS
De
19% 19% NS
Ra
AV
30% 30% NS
DT
16% 16% NS

Contrary to expectations, dividing the species according to their reproductive modes did not increase the explanatory power of the MRM models. Nevertheless, it is possible to notice some differences among groups. Species with aquatic reproduction had 24% of total variation explained by environmental and geographical distance in *terra firme* forests (only envi= 3% and only geo=15% and interception=6%), but only 2% of turnover explanation was related to any of our measures in *várzea* forests (fully due to geographical distance). At the local scale, the environmental component was significant in Tapajós (38%), Amanã (19%), Amapá (11%) and Caxiuanã (7%), whereas the spatial component was only significant in Tapajós (29%) and Caxiuanã (2%). Turnover of species with reproduction on vegetation above the water was mainly explained by environmental factor variation, and the spatial component was significant only in *terra firme* forests (regional scale) and Amapá (local scale). For anurans that breed terrestrially, the spatial component was significant in both *terra firme* and *várzea* forests but with low explanatory power (R^2= 5% and 4% respectively), and at the local scale, it was only significant in Amapá (R^2= 27%; Table 1).

Species response curves along environmental gradients (HOF models)

HOF models were calculated for 11–16 species per study area (Table 2). Model I (no relationship between species occurrence and the environmental gradient) was the most common in all of the study sites (Figure 5). As expected, areas with a higher proportion of species showing occurrence curve of model II (linear) were the same ones that had higher r^2 values in the species turnover analyses (Figure 5 and table 1). The proportion of species with monotonic or unimodal response shapes (HOF model II, III, IV and V) to an environmental gradient was 52.4%, 34.4%, 39.5%, 30.3% and 38.8% in Amapá, Caxiuanã, Tapajós, Mamirauá and Amanã, respectively.

Species response to the same gradient varied among areas (e.g. *Adenomera andreae* showed model I= no response to all of the variables in Tapajós, but responded in different ways in other areas). Also, the same variable presented distinct importance to species according to the area tested (e.g. most of the species occurrence probability to day temperature was modeled according to models II - VI in Amapá, while in Tapajós most of the species presented no response to that variable).

Table 2. Final HOF model selected after 999 permutations (the most common) according to each site at local scale. Species shown are the ones with occurrence in at least five plots for each of the eleven continuous variables. DT: Day temperature; NT: Night temperature; DM: Day moisture; NM: Night moisture; CO: Canopy openness; LD: Leaf litter depth; CB: Circumference at breast high; TA: Number of tree stems; WW: Watercourse width; WD: Watercourse depth; WV: Water velocity. Light gray lines= terrestrial breeders, Dark gray= vegetation breeders, White lines= aquatic breeders.

	HOF models						
	I	II	III	IV	V	VI	VII
				Amapá			
Adenomera andreae	CO, NT, LD, CBH	DT, TA, WW, WV		DM	NM	WD	
Osteocephalus oophagus	CO	NM, CB, TA, WV		WW, WD		DT, NT, DM	LD
Pristimantis marmoratus	CO, WV	DT, LD, TA, WW		DM	NM	NT	CB, WD
Dendropsophus minimus	CO, LD, CB	DT, TA, WV		DM	NM	NT, WW, WD	
Hyalinobatrachium fleischmanni	CO, NT, LD, CB	WV	DT	DM, WW	NM	TA, WD	
Phyllomedusa vaillantii	CO, NM, CB, WW, WD	NT, LD, WV		DT, DM, TA			
Hypsiboas dentei	DT, WW	NM, CO, CB, TA, WD	NT	WV		DM, LD	
Hypsiboas geographicus	NM, WD	DT, NT, DM, CB		CO, TA, WW, WV			LD
Leptodactylus mystaceus	CO, NT, DM, NM	DT, LD, CB, TA, WW, WD		WV			
Leptodactylus petersii	DT, NM, CB, WD, WV	DM, CO, LD, TA, WW				NT	
Osteocephalus leprieurii	NM, LD, TA, WD, WV	NT, DM, CO, WW		TA		DT	
Osteocephalus taurinus	NT, DM, CB	WW, WD	DT	CO, WV		NM	LD
Rhinella gr. *margaritifera*	CO, DT, NT, DM, NM, LD, TA, WW, WV	CB, WD					
				Caxiuanã			
Adenomera andreae	NM, LD, CB, TA	DT, DM, WW				NT, CO, WD	
Allobates gr. *trilineatus* sp2	CB	DM, NM, CO, WD		NT, LD, TA	WW	DT	
Amazophrynella bokermanni	DT, DM, CO, TA, WW, WD	LD				NT, NM, CB	
Dendropsophus brevifrons	NT, CO, WD	DT, NM		LD, CB		DM	TA, WW
Dendropsophus minimus	DT, NM, CO, CB, WW	TA		WD		NT, DM, LD	
Dendropsophus minusculus	DT, DM, NM, LD, TA, WW, WD	CO				NT, CB	
Hyalinobatrachium mondolfii	DT, DM, WW, WD	NM, TA				CO, LD, CB	NT
Phyllomedusa vaillantii	NT, WW			CO, TA		DM, NM, WD	DT, LD, CB
Vitreorana oyapiensis	DT, NT, CO, TA, WW	DM, NM, LD, CB				WD	
Hypsiboas calcaratus	DM, NM, CO, CB			LD, TA		NT, WW, WD	DT
Hypsiboas cinerascens	DT, CO, CB, TA, WD	NT, LD		WW		DM, NM	
Hypsiboas geographicus	DM, NM, WW, WD	LD	DT, CB		TA	NT, CO	
Leptodactylus knudseni	WD	NT, CO		DM, NM, LD, CB, WW		DT	TA
Leptodactylus petersii	DM, NM, CO	DT, NT, WD	LD	CB	TA	WW	

Osteocephalus taurinus	NT, LD, CB, TA, WW, WD	DT, DM, CO				NM	
Rhinella castaneotica	NT, NM, TA	DT, CO, LD, WD				DM, CB, WW	

Tapajós

Adelphobates castaneoticus	NT, DM, CB, TA, WW	CO, LD, WV		WD		DT	NM
Adenomera andreae	DT, NT, DM, NM, CO, LD, CB, TA, WW, WD, WV						
Allobates gr. *trilineatus*	DM, CO, LD, WV	CB, TA, WD				DT, NT, WW	NM
Leptodactylus pentadactylus	DT, NT, CO, CB, TA, WW, WV	WD	NM	DM		LD	
Pristimantis fenestratus	DT, CO, TA	DM, NM, LD, CB, WV		WD		NT, WW	
Amazophrynella bokermanni	DT, NT, DM, CO, LD, CB, TA, WD, WV	WW				NM	
Engystomops freibergi	DT, NT, DM, CO, LD, CB, WD, WW, WV	TA					
Hyalinobatrachium mondolfii	DT, NT, DM, NM, CB	CO, TA, WW, WD		WV		LD	
Vitreorana oyapiensis	DT, NT, DM, NM, CB	CO, LD, WW, WD		TA, WV			
Chiasmocleis hudsoni	NM, TA	DT, LD, CB, WW, WV		CO, WD	NT	DM	
Hypsiboas boans	DT, NT	CB		DM, LD, WD, WV	CO	NM, TA, WW	
Hypsiboas cinerascens	DT, DM, NM, LD, WD	NT, CO, CB, TA, WW				WV	
Hypsiboas geographicus	DT, NT, CO, CB	TA, WD		DM, LD, WW	WV	NM	
Osteocephalus taurinus	DM, NM, CO, CB	DT, NT, LD, WD, WV		WW		TA	

Mamirauá

Adenomera hylaedactylus	LD, TA	DT, NT, CO, WW, WD				DM	CB
Allobates crombiei	NT, DM, CO, CB, TA, WW	WD				LD	DT
Leptodactylus pentadactylus	DT, DM, CO, LD, WW, WD	NT				CB, TA	
Hypsiboas dentei	NT, LD	DT, CO, TA		WW, WD			DM, CB
Hypsiboas fasciatus	CB, TA	DT, NT, CO, LD, WW, WD				DM	
Hydrolaetare sp.	DT, DM, LD, TA	NT, CO				WW, WD	CB
Leptodactylus petersii	DT, DM, LD, CB, TA, WW, WD	CO				NT	
Osteocephalus leprieurii	DT, CO			NT, WD	LD	DM, WW	CB, TA
Rhinella lescurei	CO, LD, CB, TA, WW, WD	NT				DT, DM	
Scinax garbei	DT, DM, CO, LD, WW, WD	NT	CB			TA	
Scinax nebulosus	CB, WW, WD	DT		NT, TA		DM, CO	LD

Amanã

Ameerega hahnelli	NT	DT		CO, LD		DM, NM, TA	CB
Leptodactylus pentadactylus	LD	NT, DM, NM, CO, CB		DT		TA	
Dendropsophus miyatai	NT, DM, NM, LD, CB, TA	CO				DT	
Dendropsophus rossalleni	CB	DT, CO, LD	NM			NT, DM, TA	
Leptodactylus petersii	DM, NM, CO, LD	DT, NT, CB, TA					
Rhinella lescurei	DT, NT, DM, NM, CO, LD	CB, TA					
Rhinella marina	DT, NT, DM, NM, CO, LD, TA						CB
Scinax nebulosus	NM, CB			NT, CO, LD		DT, DM	TA

Scinax gr. *rostratus*	DT, DM, NM, LD, CB, TA	CO	NT	
Scarthyla goinorum	NT, CO	LD, CB, TA	DM, NM	DT

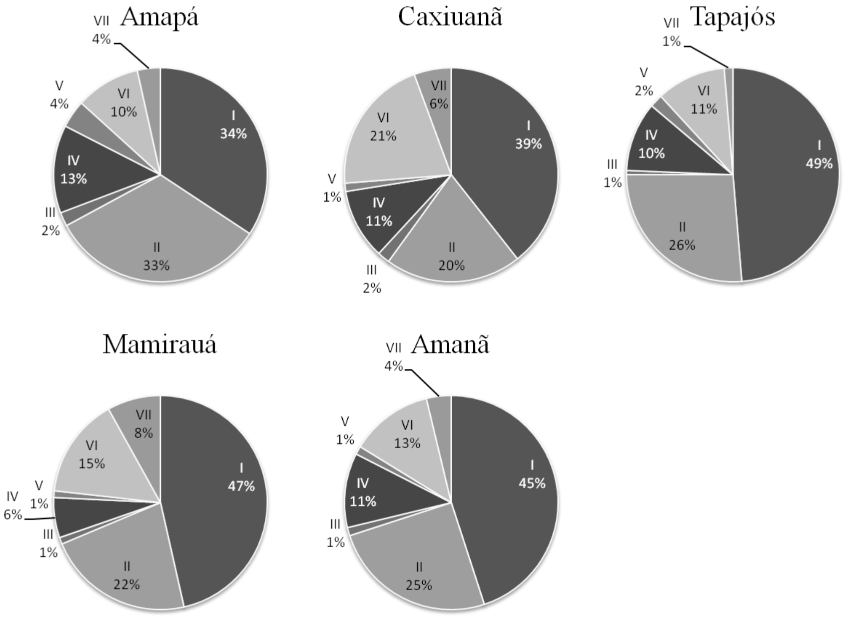


Figure 5. Number of times each HOF model appeared per area on each of the eleven continuous variables measured in Amazonia, Brazil.

DISCUSSION

Species reproductive modes and habitat heterogeneity

When comparing the frog communities in *terra firme* and *várzea* forests, we found that the proportion of species that lay their eggs in water was higher in *várzea* (70% vs. 55%), and the proportion of species with fully terrestrial breeding was higher in *terra firme* (25% vs. 14%). This was according to our expectations, because the prevalence of small ponds and other suitable water bodies is higher in seasonally inundated forests than in non-inundated forests. The prevalence of fully aquatic breeders over *várzea* forests might be a response to the characteristics of the water bodies and the intense annual flooding regime of the rivers. *Várzea* forests present an average amplitude of flooding about 10 m (Junk 1989) that probably act as an environmental filter, facilitating the establishment of aquatic breeding anurans. It's exactly the flooding characteristics that make várzea forests and Caxiuanã, classified as *terra firme*, so similar. Due to the flat terrain on the margin of the streams, part of the forest in Caxiuanã get inundated on the rainy season, but the flooding high isn't much higher than 1 meter (Montag *et al.* 2013, personal observation). If the amplitude of flooding is not so high, the understory become a suitable environment to species that use it to laying eggs, even when it's inundated, favoring species with this reproduction. Actually, when the forest is not inundated and the water is restricted to the main stream, this environment becames not available to this species group.

The same pattern of breeding modes is also apparent when comparisons are done at the local scale. The proportion of species reproducing directly on the water was high in the seasonally inundated Mamirauá (70%) and Amanã (65%), but lower in Caxiuanã (54%). On the other hand, the proportion of species laying their eggs in the vegetation was higher in Caxiuanã (27% vs. 10% and 19% in Mamirauá and Amapá, respectively; Figure 3). Anuran species with eggs and tadpoles that develop out of water are common in Amazonia (Hödl 1990; Magnusson & Hero 1991). The diversity of reproductive modes that do not totally depend on the water tends to be higher in very humid environments and areas with greater diversity of microhabitats (Duellman 1989, Hödl 1990, Haddad & Prado 2005, Pombal & Haddad 2005). Although laying eggs directly on the water is the most common and general reproductive mode to anurans worldwide (Duellman & Trueb 1986), it's expected that in areas with higher hydric stress (e.g. open or disturbed areas) the proportion of species with this reproductive mode would be even higher when compared to forested environments (Vieira *et al.* 2009, Bitar *et al.* 2012).

The intense flooding regime and the high proportion of aquatic breeders in *várzea* forests were some of the reasons that led us to believe that this habitat was more structurally homogeneous than *terra firme* forests. Although *várzea* forests are seasonally under the flooding effect, according to the environmental variables measured here from water bodies and their surrounding area, they are not less spatially heterogeneous than *terra firme* forests. But despite the similar heterogeneity between those two habitats, the environmental characteristics and consequently the reproductive microhabitats available to frogs are completely different (Figure 4). Habitat homogeneity was also the reason claimed to justify the great occurrence of anuran species that exhibit aquatic eggs and larvaes on another two flooded environments in South America, Pantanal with 62.5% of the species with aquatic reproduction (Prado *et* *al.* 2005) and Chaco region with 50% (Perotti, 1997). Nevertheless, according to the environmental variables that we measured here from the breeding habitats and their surrounding areas, *várzea* were as environmentally heterogeneous as *terra firme* forests. Indeed, several well-defined forest types are distributed along the flood gradient in *várzea* forests, and they differ in forest structure, tree species composition and richness (Assis & Wittmann 2011).

Spatial x environmental processes and reproductive characteristics

In general, it can be expected that species turnover is affected both by environmental differences and by other processes related to spatial distance. The interesting question is: which environmental variables are relevant, and to what degree can the observed patterns be explained by the alternative variables in any particular case? We found that the answer varied both among amphibians with different breeding modes and among study areas and habitat types (Table 1). At the broadest extent, the spatial component of the turnover was much higher than the environmental component. Bitar *et al.* (chapter 2) have already observed this for the terra firme forests, and here we report that the same holds for varzea forests, independently of the reproductive mode of the frogs. This is logical, because many environmental variables are spatially autocorrelated over large extents (Steinitz *et al.* 2006), and the low dispersal ability of amphibians becomes evident in that many species may have ranges that do not extend over all areas (Smith & Green 2005, Qian 2009). Historical effects and the presence of barriers to anuran dispersion, such as large rivers, may also contribute to the high explanatory power of geographical distances when analyzing broad-scale species turnover (Amazonian scale). Even though our data are focused on present-day patterns and we cannot confirm or directly test biogeographical hypothesis, geographical distance may appear important in the analyses because it indirectly correlates with some historical patterns.

Additionally, Zeisset & Beebee (2008) argue that a combination of five hypothesis could explain current patterns of frogs distribution in South America: "(a) Changing distributions of land and sea or in the landscape due to tectonic movements or sea level fluctuations (the Palaeogeography hypothesis); (b) Barrier effects of

Amazonian rivers (the River hypothesis); (c) The existence of isolated refugia during dry climatic periods of the Tertiary and Quaternary (Refuge hypothesis); (d) A combination of barrier effects of broad rivers and vegetational changes during periods of aridity (the Climatic/River refuge hypothesis); (e) Competitive interactions between species during the cool periods of the Pleistocene (the disturbance vicariance hypothesis)". For example, the distribution of *Allobates femoralis* is linked to an old mountain range, that associated to the low dispersal ability of the species resulted in genetic divergence between areas that not show an obvious barrier limiting the current distribution of the species (Lougheed *et al.* 1999). Even though it is hard to predict distribution patterns over extensive areas of relatively stable tropical forests, it seems that lowland species distribution is better explained by an combination of two main hypothesis, the palaeogeographical and river as barriers (Zeisset & Beebee 2008). So, since all *várzea* plots are distributed on the same interfluve (area of endemism) and the total extent is smaller than the observed among sampled *terra firme* forests, it could explain the low importance of geographical distance to frogs turnover in *várzea* forests.

Differences between *terra firme* and *várzea* forests have not been tested to date, and only Bitar *et al.* (Chapter 2) have accounted for differences among areas within *terra firme* environments at the local scale. In that study, authors studied frog communities in different areas at the same scale, and also found considerable variation in vegetation structure and frog community characteristics, which could lead to differences in turnover partition patterns among areas (Bitar *et al.* chapter 2). This suggests that extrapolating results found in a single area to other tropical forests considered environmentally similar can be risky (Tews *et al* 2004, Ernst & Rödel 2008, Keller *et al.* 2009, Bitar *et al.* 2014). Al-Shami *et al.* (2013) observed differences in the turnover of macroinvertebrate communities among streams from distinct basin drainages and related it to historical factors that may be affecting the patterns observed nowadays. Amazonia has been suggested to be a mosaic of distinct areas of endemism separated by the major rivers, each with their own evolutionary relationships and biotic assemblages (Silva *et al.* 2005). Those areas, initially detected for primates (Wallace 1852, Silva & Oren 1996) and birds (Haffer 1978, 1985, 1987), have also been identified for lizards (Ávila-Pires 1995) and frogs (Ron 2000). Comparing the distribution of 335 frog species in Amazonia with the distribution of lizards and primates, Ron (2000) found strong congruencies with areas of endemism, and they should be the basic geographic unit considered in ecological studies and for the creation of conservation corridors of contiguous protected areas (Silva *et al.* 2005). Our sampling areas are very distant from each other, located in distinct areas of endemism, separated by large rivers and other vicariant processes. Thus, results on turnover partition patterns between environmental dissimilarity and spatial distance may have been influenced by the location of the sampling areas. We strongly recommend studies comparing areas at the same scale and with the same area of endemism to check how communities will respond.

Our results suggest a more consistent turnover pattern among species with the same reproductive mode than among areas of the same vegetation type, especially in *terra firme* forests. Landeiro *et al.* (2014) already documented the importance of reproductive mode. They reported that aquatic breeding frogs tended to respond more strongly to variation in environmental conditions, whereas terrestrial breeders presented a spatially structured distribution (Landeiro *et al.* 2014). We indeed found that species turnover of terrestrial breeders was to a large degree explained by geographical distances at the broadest spatial extent. However, at the regional scale the geographical and environmental distances were equally important (although the environmental fraction was higher in *várzea* forests) and at local scale the spatial fraction was not even significant in most study areas.

If our results had agreeded to the observed in Central Amazonia, where aquatic breeder frogs responded mainly to changes in environmental variability and terrestrial breeders were more affected by geographical distance (Landeiro *et al.* 2014), it would explain the low or none importance of the geographical component to communities in várzea forests and Caxiuanã, which present low proportion of species with that reproductive mode. However, geographical fraction was not significant in those areas even considering only terrestrial species, and the flooding regime present in those areas seems to be the most reasonable explanation. Still, we cannot rule out the possibility that those results for terrestrial breeders are a methodological artifact, since we necessarily surveyed frogs around a water body, thus, their presence may be due to stochasticity and not related to environmental suitability. On the other hand, for aquatic and vegetation breeders, the environmental component had greater importance when it was significant, in agreement to results found in Manaus, Amazonas (Landeiro *et al.* 2014) and confirming the high correspondence of this species group with their breeding habitat.

HOF models

Species response shape along gradients is directly linked to their optima and niche width (Huisman *et al.* 1993), and if many species have narrow ranges of distribution along a gradient, high turnover between sites along that gradient is expected. Therefore, variables that emerge as important in a community-level variance partitioning should also appear as important for the individual species. Conversely, if a variable is important for several species but does not appear important for the community as a whole, one might suspect that excessive gradient length or other confounding factors were at play. Our final MRM models selected only one continuous variable in Amapá (day moisture) and and two in Caxiuanã (night temperature and day moisture). The same variables were not the most significant ones (HOF models II-VII) selected in our HOF analyzes to the whole community in those areas, but they were important to specific species groups. For example, day moisture was significant for terrestrial and vegetation species in Amapá (model IV) and for vegetation species in Caxiuanã (model II). Terrestrial and vegetation breeding species depend directly on the environmental conditions to not dehydrate their eggs (Hödl 1990, Haddad & Prado 2005), so it makes sense that their distribution is linked to day moisture. However, HOF models could only be calculated to our continuous variables, and almost half variables measured here are categoricals. Moreover, all our categorical variables are related to measurements of the water characteristics, and these were the most important to predict frog turnover, especially aquatic breeders. This analytical incompatibility difficults comparisons between HOF models and species turnover with our data.

Among species that were frequent enough to be analysed (appeared in at least five sampling units), we observed that model I (no relationship between species probability of occurrence) was the most common one in all areas, especially in *várzea* sites and the Tapajós area (Figure 5). Indeed, these are the categories in which variation in species turnover was not well explained with the set of measured environmental variables. Similarly, we observed higher explanatory power in the MRM analyses for those areas where the proportion of species with HOF response model II (linear relationship) was higher. The prevalence of model II in many areas may indicate that the range of values of the environmental gradients measured in the surveyed areas was relatively small in relation to species tolerances. Model II can be thought of as one half of a unimodal distribution model (IV or V) (Jansen & Oksanen 2013). On the other hand, it may also be related to the analysis we used to calculate turnover, a linear multiple regression on distance matrices (Lichstein 2007). If we consider only those species with some response to environmental gradients, species with unimodal response shapes (models IV to V) were the majority in all areas, with Amapá presenting the highest proportion followed by Tapajós, Amanã, Caxiuanã and Mamirauá.

Because animals are affected by many kinds of environmental factors, and some of these have complex effects through animal behavior, it can be difficult to identify the most relevant variables to explain animal distributions. Tropical rainforests also lack such clear gradients that would make it easy to choose a single variable that most influences species turnover, which seems instead to be affected by a set of many variables acting together. In that sense, a multivariate approach would be more suitable to identify variables explaining community similarity and correlations between HOF models and species turnover (Ovaskainen & Soininen 2011).

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REFERENCES

Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62(1): 245–253.

Arita, H. T. & P. Rodríguez. 2002. Geographic range, turnover rate, and the scaling of species diversity. *Ecography* 25: 541-553.

Assis, R.L. & Wittmann, F. 2011. Forest structure and tree species composition of the understory of two central Amazonian várzea forests of contrasting flood heights. *Flora* 206: 251-260.

Austin, M.P. 1985. Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics* 16: 39-61.

Bitar, Y.O.C., Pinheiro, L.P.C., Abe, P.S. & Santos-Costa, M.C. 2012. Species composition and reproductive modes of anurans from a transitional Amazonian forest, Brazil. *Zoologia* 29: 19–26.

Bitar, Y.O.C; Juen, L.; Pinheiro, L.C. & Santos-Costa, M.C. 2014. Anuran Beta Diversity in a Mosaic Anthropogenic Landscape in Transitional Amazon. *Journal of Herpetology* 48(4) *In press.*

Buckley L.B. & Jetz W. 2008. Linking global turnover of species and environments. *Proceedings of the National Academy of Science* 105: 17836-17841.

Crump, M.L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. *Occasional Papers of the Museum of Natural History University of Kansas* 3: 1-62.

Crump, M. & Scott, N. 1994. Visual encounter surveys. pp 84-92. In: Heyer, W. *et al.* (eds). *Measuring and monitoring biological diversity—standard methods for amphibians*. Smithsonian Inst. Press, Washington.

Duellman, W.E. 1989. Alternative life-history styles in anuran amphibians: Evolutionary and ecological implications. In: Bruton, M.N. (ed) *Alternative Life-History Styles of Animals*. Dordrecht (The Netherlands): Kluwer Academic, pp. 102–126.

Ernst, R. & Rödel, M.O. 2008. Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environmental effects in disturbed and undisturbed forests. *Journal of tropical ecology* 24 (2): 111- 120.

Feder, M.E. & Burggren, W.W. 1992. *Environmental Physiology of the Amphibians*. University of Chicago Press, Chicago, 472p.

Giaretta, A.A.; Facure, K.G.; Sawaya, R.J.; Meyer, J.H.M. & Chemin, N. 1999. Diversity and abundance of litter frogs of a montane forest in southeastern Brazil: seasonal and altitudinal changes. *Biotropica* 31(4): 669-674.

Haffer, J. 1978. Distribution of Amazon birds. Bonner Zoologischen Beiträge 29**:**38–78.

Haffer, J. 1985. Avian zoogeography of the Neotropical lowlands. *Neotropical Ornithology* 36**:**113–146.

Haffer, J. 1987. Biogeography of Neotropical birds. in: Whitmore, T.C. & Prance, G.T. (Ed) Biogeography and Quaternary history in tropical America. Clarendon Press, Oxford, United Kingdom, pp 105-150.

Harris, M.P.K.; Allen, K.A.; McAllister, H.A.; Eyre, G.; Le Duc, M.G. & Harris, R.H. 2011. Factors affecting moorland plant communities and component species in relation to prescribed burning. *Journal of Applied Ecology* 48: 1411-1421.

Haddad, C.F.B. & Prado, C.P.A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil. *BioScience* 55(3):207-217.

Halverson, M.A.; Skelly, D.K.; Kiesecker, J.M. & Freidenburg, L.K. 2003. Forest mediated light regime linked to amphibian distribution and performance. *Oecologia* 134(3): 360-364.

Hödl, W. 1990. Reproductive diversity in Amazonian lowland frogs. *Fortschritte der Zoologie* 38: 41–60.

Huisman, J.; Olff, H. & Fresco, L.F.M. 1993. A hierarchical set of models for species response analysis. *Journal of Vegetation Science* 4**,** 37-46.

IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 11 December 2014.

Jansen, J. 2015. Hierarchical species response curves in package eHOF. Available in <http://cran.r-project.org/web/packages/eHOF/vignettes/eHOF.pdf>

Jansen, F. & Oksanen, J. 2013. How to model species responses along ecological gradients - Huisman-Olff-Fresco models revisited. *Journal of Vegetation Science* 24, 1108-1117.

Junk, W.J. 1989. Flood tolerance and tree distribution in central Amazonian flood-plains. In: Holm-Nielsen, L.B.; Nielsen, I.C.; Balslev, H. (eds.). *Tropical Forests: Botanical Dynamics, Speciation and Diversity*. Academic Press, New York, pp. 47–64.

Keller, A.; M-O. Rödel; K.E. Linsenmair & Grafe, T.U. 2009. The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. *Journal of Animal Ecolology* 78 (2): 305-314.

Landeiro, V. L.; Waldez, F & Menin, M. 2014. Spatial and environmental patterns of Amazonian anurans: Differences between assemblages with aquatic and terrestrial reproduction, and implications for conservation management. *Natureza & Conservação* 12 (1): 42-46.

Legendre, P. & Legendre, L. 1998. Numerical ecology. 2nd English edition. Elsevier, Amsterdam.

Legendre, P.; Lapointe, F. & Casgrain, P. 1994. Modeling brain evolution from behavior: A permutational regression approach. *Evolution* 48: 1487-1499.

Lichstein J. 2007. Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecology* 188:117–131.

Lougheed, S.C.; Gascon, C.; Jones, D.A.; Bogart, J.P. & Boag, P.T. 1999. Ridges and rivers: a test of competing hypotheses of Amazonian diversification using a dart-poison frog (Epipedobates femoralis). *Procedings of Royal Society of London* B 266: 1829–1835.

Magnusson, W.E. & Hero, J.M. 1991. Predation and evolution of complex oviposition behaviour in Amazon rainforest frogs. *Oecologia* 86: 310–318.

Manly, B.F. 1986. Randomization and regression methods for testing for associations with geographical, environmental and biological distances between populations. *Researches on Population Ecology* 28: 201–218.

Menin**,** M**.**; Waldez, F. & Lima, A.P. 2011. Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia. *Herpetological Journal* 21: 255-261.

Menin, M.; Lima, A.P.; Magnusson, W.E. & Waldez, F. 2007. Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns. *Journal of Tropical Ecology* 23: 539–547.

Montag, L.F.A.; Freitas, T.M.S.; Benone, N.L.; Ferreira, C.P.; Wosiacki, W.B.; Barthem, R.B. 2013. Ecologia de peixes em um “quase-lago” da Amazônia Oriental. In: Pedro Luis Braga Lisboa (org.). Caxiuanã: paraíso ainda preservado. Belém: Museu Paraense Emílio Goeldi. 656p.

Murphy, H.T.; VanDerWal, J. & Lovett-Doust, J. 2010. Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters* 13: 1233–1244.

Nekola, J.C. & White, P.S. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26: 867–878.

Oksanen, J. & Minchin, P.R. 2002. Continuum theory revisited: what shape are species responses along ecological gradients? *Ecological Modelling* 157: 119–129.

Ovaskainen, O & Soininen, J. 2011. Making more out of sparse data: hierarchical modeling of species communities. *Ecology* 92(2): 289-295.

Pavoine S.; Vallet, J.; Dufour, A.-B.; Gachet, S. & Daniel, H. 2009. On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos* 118, 391–402.

Peper, J.; Jansen, F.; Pietzsch, D. & Manthey, M. 2011. Patterns of plant species turnover along grazing gradients. *Journal of Vegetation Science* 3: 457–466.

Perotti, M.G. 1997. Reproductive modes and quantitative reproductive parameters of an anuran assemblage from the semiarid Chaco, Salta, Argentina. *Revista Chilena de Historia Natural* 70: 277-288.

Pombal Jr, J.P. & Haddad, C.F.B. 2005. Estratégias e modos reprodutivos de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil. *Papéis Avulsos de Zoologia* 45(15): 201-213.

Prado, C.P.A; Uetanabaro, M. & Haddad, C.F.B. 2002. Description of a new reproductive mode in *Leptodactylus* (Anura, Leptodactylidae), with a review of the reproductive specialization towards terrestriality in the genus. *Copeia* 2002: 1128–1133.

Prado, C.P.A.; Uetanabaro, M. & HADDAD, C.F.B. 2005. Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphibia-Reptilia* 26(2): 211-221.

Provete, D.B.; Gonçalves-Souza, T.; Garey, M.V.; Martins, I.A. & Rossa-Feres, D.C. 2014. Broad-scale spatial patterns of pond morphology and canopy cover affect the structure of Neotropical tadpole metacommunity. *Hydrobiologia* 734(1):69-79.

Qian, H. 2009. Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. *Journal of Systematics and Evolution* 47: 509-514.

Qian, H. & Ricklefs, R.E. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography* 21: 341-351.

Ribeiro Jr, J.W.; Lima, A.P. & Magnusson, W.E. 2012. The Effect of Riparian Zones on Species Diversity of Frogs in Amazonian Forests. *Copeia* 3: 375-381.

Ron, S. 2000. Biogeographic area relationships lowland Neotropical rainforest based on raw distribution of vertebrate group. *Biological Journal of Linnean Society* 71: 379-402.

Rydgren, K.; Økland, R.H. & Økland, T. 2003. Species response curves along environmental gradients. A case study from SE Norwegian swamp forests. *Journal of Vegetation Science* 14(6): 869–880.

Silva, J.M.C. & Oren, D.C. 1996. Application of parsimony analysis of endemicity (PAE) in Amazonian biogeography: an example with primates. *Biological Journal of the Linnean Society* 59(4): 427-437.

Silva J.M.C.; Rylands, A.B. & Fonseca, G.A.B. 2005. O destino das áreas de endemismo da Amazônia. *Megadiversidade* 1:124-131.

Silva, F.R.; Almeida-Neto, M; Prado, V.H.M.; Haddad, C.F.B & Rossa-Feres, D.C. 2012. Humidity levels drive reproductive modes and phylogenetic diversity of amphibians in the Brazilian Atlantic Forest. *Journal of Biogeography* 39(9): 1720–1732.

Smouse, P.E.; Long, J.C. & Sokal, R.R. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* 35: 627 – 632.

Smith, M.A. & Green, D.M. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28: 110-128.

Souza, V.M.; Souza, M.B. & Morato, E.F. 2008. Efeitos da sucessão florestal sobre a anurofauna (Amphibia: Anura) da Reserva Catuaba e seu entorno, Acre, Amazônia sul ocidental. *Revista Brasileira de Zoologia* 25**:** 49-57.

Steinitz, O.; Heller, J.; Tsoar, A.; Rotem, D. & Kadmon, R. 2006. Environment, dispersal and patterns of species similarity.*Journal of Biogeography* 33: 10441054.

Tews, J.; Brose, U.; Grimm, V.; Tielborger, K.; Wichmann, M.C.; Schwager, M. & Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79–92.

Tuomisto, H. & Ruokolainen, K. 1997. The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. *Biodiversity and Conservation* 6**:** 347-357.

Tuomisto, H., Ruokolainen, L. & Ruokolainen, K. 2012. Modelling niche and neutral dynamics: on the ecological interpretation of variation partitioning results. *Ecography* 35: 961-971.

Tuomisto, H.; Ruololainen, K. & Yli-Halla, M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299: 241-244.

Vonesh, J.R. 2001. Patterns of richness and abundance in a tropical leaf-litter herpetofauna. *Biotropica* 33**:** 502-510.

Wallace, A.R. 1852. On the Monkeys of the Amazon. *Proceedings of the Zoological Society of London* 20: 107-10.

Wittmann, F.; Junk, W.J. & Piedade, M.T.F., 2004. The *várzea* forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. *Forest Ecology and Management* 196, 199–212.

Zeisset, I. & Beebee, T. 2008. Amphibian phylogeography: a model for understanding historical aspects of species distributions. *Heredity* (Edinb) 101: 109–19.

Zimmerman, B.L. & Bierregaard, R.O. 1986. Relevance of the Equilibrium Theory of Island Biogeography and Species-Area relations to Conservation with a case from Amazonia. *Journal of Biogeography* 13: 133-143.

Zimmerman, B.L. 1994. Audio strip transects. In*:* Heyer, W.R.; Donnelly, M.A.; McDiarmid, R.W.; Hayek, L.A.C. & Foster, M.S. (eds.) *Measuring and Monitoring Biological Diversity*. Smithsonian Institution Press, Washington and London, p.92-97.

APPENDIX I

Local of species occurrence and their respective reproductive mode

		Terra firme			*Várzea*	
Taxa	Reproductive mode	Amapá	Caxiaunã	Tapajós	Mamiruá	Amanã
Allphrynidae						
Allophryne ruthveni	A	1	0	0	0	0
Aromobatidae						
Allobates crombiei	T	0	0	0	1	1
Allobates femoralis	T	1	0	1	0	0
Allobates gr. *trilineatus*	T	0	0	1	0	0
Allobates gr. *trilineatus* sp2	T	0	1	0	0	0
Allobates gr. *trilineatus* sp3	T	0	0	0	1	0
Allobates gr. *trilineatus* sp4	T	0	0	0	1	0
Allobates gr. *trilineatus* sp5	T	0	0	0	0	1
Bufonidae						
Amazophrynella bokermanni	AV	0	1	1	0	0
Amazophrynella minuta	AV	1	0	0	0	1
Atelopus hogmooedi	A	1	0	1	0	0
Rhaebo guttatus	A	1	0	0	0	0
Rhinella castaneotica	A	0	1	1	0	0
Rhinella gr. *margaritifera*	A	0	0	0	1	1
Rhinella lescurei	A	1	0	0	0	0
Rhinella marina	A	1	0	1	1	1
Centrolenidae						
Hyalinobatrachium fleischmanni	AV	1	0	0	0	0
Hyalinobatrachium mondolfii	AV	0	1	1	0	0
Hyalinobatrachium sp.	AV	0	0	1	0	0
Vitreorana oyapiensis	AV	0	1	1	0	0
Ceratophryidae						
Ceratoprhys cornuta	A	1	1	0	0	0
Craugastoridae						
Pristimantis chiastonotus	T	1	0	0	0	0
Pristimantis fenestratus	T	0	0	1	0	0
Pristimantis marmoratus	T	1	0	0	0	0
Dendrobatidae						
Adelphobates castaneoticus	T	0	0	1	0	0
Ameerega hahnelli	T	0	0	0	1	1
Ameerega pulchripecta	T	1	0	0	0	0
Ranitomeya ventrimaculata	T	0	1	0	0	0
Hylidae						
Dendropsophus brevifrons	AV	1	1	0	0	0
Dendropsophus leucophylatus	AV	0	0	0	1	1

Dendropsophus minimus	AV	1	1	0	0	0
Dendropsophus minusculus	AV	1	1	0	0	0
Dendropsophus miyatai	A	0	0	0	1	1
Dendropsophus parviceps	A	0	0	0	1	0
Dendropsophus rhodopeplus	A	0	0	0	1	1
Dendropsophus rossalleni	AV	0	0	0	1	1
Dendropsophus sp. nov.	AV	1	0	0	0	0
Dendropsophus sp2. nov.	AV	0	0	1	0	0
Dendropsophus sp3. nov.	AV	0	0	0	1	1
Dendropsophus triangulum	AV	0	0	0	0	1
Hypsiboas boans	A	1	0	1	0	1
Hypsiboas calcaratus	A	1	1	0	1	1
Hypsiboas cinerascens	A	0	1	1	0	0
Hypsiboas dentei	A	1	0	0	1	0
Hypsiboas fasciatus	A	0	0	0	1	0
Hypsiboas geographicus	A	1	1	1	1	0
Hypsiboas lanciformis	A	0	0	0	1	1
Hypsiboas leucocheilus	A	0	0	1	0	0
Hypsiboas ornatissimus	A	1	0	0	1	0
Hypsiboas punctatus	A	0	0	0	0	1
Hypsiboas wavrini	A	0	0	1	0	0
Osteocephalus inframaculatus	A	0	0	1	0	0
Osteocephalus leprieurii	A	1	0	0	1	1
Osteocephalus oophagus	T*	1	0	1	0	0
Osteocephalus taurinus	A	1	1	1	1	0
Phyllomedusa bicolor	AV	1	0	0	0	0
Phyllomedusa vaillantii	AV	1	1	1	0	0
Scarthyla goinorum	A	0	0	0	0	1
Scinax boesemani	A	0	0	1	0	0
Scinax cf. cruentommus	A	1	0	0	0	0
Scinax cf. x-signatus	A	0	0	1	0	0
Scinax garbei	A	0	0	1	0	0
Scinax gr. *rostratus*	A	0	0	0	1	1
Scinax gr. *ruber* sp.1	A	0	0	0	1	1
Scinax nebulosus	A	0	1	1	0	0
Scinax rostratus	A	0	0	0	1	1
Scinax sp. 1	A	1	0	0	0	0
Scinax sp. nov.	A	0	0	0	1	0
Sphaenorhyncus carneus	A	0	0	0	0	1
Sphaenoryncus dorizae	A	0	0	0	0	1
Trachycephalus coriaceus	T*	1	0	0	0	0
Trachycephalus hadroceps	T*	0	1	0	0	0
Trachycephalus resinifictrix	A	0	1	0	0	0
Leiuperidae						
Engystomops freibergi	A	0	0	1	0	0

Leptodactylidae						
Adenomera andreae	T	1	1	1	0	0
Adenomera hylaedactylus	T	0	0	0	1	1
Hydrolaetare schmidti	A	0	0	0	1	1
Leptodactylus knudseni	A	1	1	0	0	0
Leptodactylus leptodactyloides	A	1	0	0	0	0
Leptodactylus latrans	A	0	0	0	1	0
Leptodactylus mystaceus	A	1	1	0	0	0
Leptodactylus paraensis	T	0	1	1	0	0
Leptodactylus pentadactylus	T	1	0	1	1	1
Leptodactylus petersii	A	1	1	1	1	1
Leptodactylus rhodomystax	A	1	1	0	0	0
Leptodactylus stenodema	T	1	0	0	0	0
Microhylidae						
Chiasmocleis hudsoni	A	0	1	1	1	0
Chiasmocleis shudikarensis	A	1	0	0	0	0
Chiasmocleis sp. nov.	A	1	0	0	0	0
Ctenophryne geayi	A	0	0	0	1	0
Hamptophryne boliviana	A	1	0	0	0	0
Pipidae						
Pipa pipa	A	0	1	1	0	0