

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA-INPA
Programa de Pós-Graduação em Ecologia

**PADRÕES DE DISTRIBUIÇÃO DE ANUROS EM UMA ÁREA DE 25 KM² EM UMA
FLORESTA SAZONALMENTE ALAGÁVEL NO NORTE DA AMAZÔNIA
BRASILEIRA**

Paula Coca Soto

MANAUS-AM

Agosto, 2010

Paula Coca Soto

**PADRÕES DE DISTRIBUIÇÃO DE ANUROS EM UMA ÁREA DE 25 KM² EM UMA
FLORESTA SAZONALMENTE ALAGÁVEL NO NORTE DA AMAZÔNIA
BRASILEIRA**

Orientadora: Dra. Claudia Keller
Co-orientador: Dra. Albertina Pimentel Lima

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

Manaus, Amazonas

Agosto, 2010

BANCA JULGADORA DO TRABALHO ESCRITO

Dra. Cynthia Peralta de Almeida Prado

(Universidade Estadual Paulista Júlio de Mesquita Filho)

Parecer: APROVADA COM CORREÇÕES

Dr. James Watling

(Florida International University)

Parecer: APROVADA COM CORREÇÕES

Dr. Marcelo Menin

(Universidade Federal do Amazonas)

Parecer: APROVADA COM CORREÇÕES

BANCA JULGADORA DA DEFESA PRESENCIAL

Dra. Regina Celi Costa Luizão

(Instituto Nacional de Pesquisas da Amazônia)

Parecer: APROVADO

Dr. Renato Cintra

(Instituto Nacional de Pesquisas da Amazônia)

Parecer: APROVADO

Dr. Thierry Ray Jehleb Gasnier

(Universidade Federal do Amazonas)

Parecer: APROVADO

C659

Coca Soto, Paula Mercedes

Padrões de distribuição de anuros em uma área de 25 Km² em uma floresta sazonalmente alagável no norte da Amazônia brasileira /

Paula Mercedes Coca Soto.--- Manaus : [s.n.], 2010.

xii, 52 f. : il. color.

Dissertação (mestrado)-- INPA, Manaus, 2010

Orientador : Claudia Keller

Co-orientador : Albertina Pimentel Lima

Área de concentração : Ecologia

1. Anuros – Ecologia – Amazônia. 2. Floresta inundável. 3. Padrões de distribuição. 4. Gradientes ambientais. I. Título.

CDD 19. ed. 597.8045

Sinopse:

Foram estudados os padrões de distribuição de anuros em uma área de 25 km² em uma floresta sazonalmente inundável. Variáveis ambientais potencialmente preditoras, como a porcentagem de argila no solo, a porcentagem de silte no solo, a proporção de área alagável e a altitude das parcelas de amostragem explicaram a variação na composição das espécies das assembléias de anuros. Fatores ambientais como textura do solo e a permanência do alagamento são efetivamente bons preditores da ocorrência de espécies de anuros por tipo de habitat.

Palavras chave: assembléias de anuros, floresta inundável, distribuição temporal e espacial, gradientes ambientais, variáveis preditoras

...Recuerdo las palabras finales, repetidas en cada redacción como un mandamiento secreto: "Así combatieron los héroes, tranquilo el admirable corazón, violenta la espada, resignados a matar o a morir".

Jorge Luis Borges
El jardín de senderos que se bifurcan-Ficciones
(1941)

AGRADECIMENTOS

À minhas orientadoras Claudia Keller e Albertina Lima por terem me acolhido como orientada, por terem me oferecido a oportunidade de trabalhar em Viruá, pela atenção, dedicação, incentivo e carinho no período do mestrado. Seu exemplo contribuiu muito para o meu crescimento profissional e pessoal. Obrigada de coração...

Ao INPA pela oportunidade de mestrado, ao CNPq pela bolsa de estudos concedida. Ao programa de Estudantes-Convênio de Pós-graduação-PEC-PG e à Embaixada de Brasil em Bolívia por ter me selecionado e oferecido a oportunidade de estudar em Brasil.

Ao Programa de Pesquisa em Biodiversidade (PPBio) pelo apoio financeiro no trabalho de campo. Agradeço especialmente a Sergio Marques e Fabrício Baccaro pelo apoio logístico.

Aos Drs. Reginaldo Machado, Vanessa Verdade, Marcelo Menin, Flávia Costa, Elizabeth Franklin e Renato Cintra pelas críticas e sugestões dadas ao projeto durante o período de avaliação e à aula de qualificação.

Aos Drs. Marcelo Menin, Cynthia Prado e James Watling pelas valiosas sugestões e comentários na avaliação da versão final da minha dissertação.

Ao pessoal do PARNA Viruá que sempre me trataram com tanto carinho, agradeço constante assistência em tudo o que eu precisava: Antonio Lisboa, Beatriz Lisboa, Onei Araújo, Iran Almeida, Marlúcia Costa e seus filhos.

Aos auxiliares de campo que trabalharam comigo Renato, Miranda, Camarão e Fiat. Agradeço especialmente a Oziel da Silva pelo companheirismo e amizade no período de amostragem 2009.

Ao Ibama pela licença concedida nº 15338-2 para trabalhar no PARNA Viruá.

À Tânia Pimentel pela disponibilização dos dados de textura do solo.

À Vinicius Carvalho pela ajuda na identificação de espécies.

À Flávia Costa e Victor Landeiro pelas constantes contribuições e discussões de estatística que me ajudaram esclarecer dúvidas fundamentais.

À Galo Coca pela paciência, e ajuda na elaboração dos mapas do Viruá.

À Beverly Franklin, Rosirene Farias, Andressa Saraiva, Erica Magalhães e Estefania Nascimento pela constante colaboração na resolução problemas nas diferentes etapas de meu período no mestrado. Obrigada...

Os amigos Denise Prado, André Nogueira, Butch Wright, Júlio do Vale, Marlos Brum, Diana Rojas, pela amizade, apoio e incentivo que me ofereceram.

Um agradecimento especial a minha família, meus pais: Josefina e Fernando e meus irmãos: Néstor e Galo que sempre me apoiaram em tudo que precisei e em tudo que quis fazer. Muito obrigada pelos momentos de carinho apesar da distância. Agradeço também a Gustavo Alvarez pelo apoio e amor neste período de distância. Amo a todos vocês.

RESUMO

Estudos recentes sobre assembléias de anuros arbóreos e de serrapilheira sugerem que a variação na composição das assembléias explicada por parâmetros ambientais é de pouca importância. Em contraste, para assembléias de anuros associados com áreas ripárias a heterogeneidade ambiental, os efeitos espaciais e os ambientes espacialmente estruturados foram considerados relevantes. Investigamos padrões de distribuição de anuros em uma área de 25 km² localizada em uma zona de mosaico de floresta de terra firme não alagável e floresta de terra firme, campinarana e campina alagáveis, situada no Parque Nacional do Viruá (Roraima, Brasil) no norte da Amazônia. Analisamos variáveis ambientais potencialmente capazes de prever a estrutura da assembléia de anuros e descrevemos a composição de assembléias de anuros em relação a gradientes ambientais em 30 parcelas distribuídas uniformemente na área de estudo. As variáveis ambientais analisadas em todas as parcelas foram textura do solo e altitude. Para parcelas sujeitas a alagamento incluímos a proporção de área alagável nas análises. Determinamos a abundância de cada espécie baseada em três períodos de amostragem durante a estação chuvosa de 2009. A variação na composição das espécies entre as parcelas foi sintetizada em dois eixos usando o método multivariado de escalonamento não métrico multidimensional (NMDS), baseado na matriz de abundâncias e de ocorrência das espécies. Usamos análises de regressão múltipla para avaliar variáveis capazes de explicar a variação na composição de espécies. Registramos 3339 indivíduos pertencentes a 19 espécies de 5 famílias. A maioria das espécies foi encontrada no início da estação chuvosa, e a maioria dos indivíduos foi registrada no meio da estação chuvosa. *Dendrosophus* sp. foi a espécie mais abundante, e *Osteocephalus* aff. *taurinus* a menos abundante. *Dendrosophus* sp., *Hypiboas* sp., e *Leptodactylus* aff. *andreae* representaram 63.8% de todos os indivíduos encontrados nas parcelas. O primeiro e o segundo eixos do NMDS ordenaram as parcelas de acordo com o gradiente de conteúdo de argila do solo. Cobertura do dossel, cobertura de herbáceas, conteúdo de areia, declividade e o número de árvores por parcela foram correlacionados com o conteúdo de argila do solo e, portanto explicaram a variação na composição da assembléia de anuros. Considerando somente as parcelas sujeitas a alagamento, o conteúdo de argila foi, também, o mais importante fator ambiental associado com a composição de anuros, produzindo uma heterogeneidade ambiental responsável pela estrutura da assembléia de anuros no PARNA Viruá. Os resultados são de interesse ecológico e de significância prática para a conservação de anuros em florestas tropicais sazonalmente alagáveis.

Palavras chave: Anura, floresta inundável, padrões de distribuição, gradientes ambientais, Norte da Amazônia.

ABSTRACT

Recent studies on arboreal and leaf litter anuran assemblages suggest that the variation in assemblage composition explained by environmental parameters is only of minor importance. In contrast, for anuran assemblages of streams habitat heterogeneity, spatial effects and spatially structured environments were considered relevant. Therefore, we investigated the patterns of distribution of anurans in an area of 25 km² in a seasonally flooded forest situated in the Viruá National Park (Roraima state, Brazil) in Northern Amazonia. We analyzed environmental variables potentially capable of predicting anuran assemblage structure and composition in relation to environmental gradients in 30 plots evenly distributed over a 5x5km area. Environmental variables with a significant effect in all plots were soil texture and altitude. For plots subject to flooding we included water cover in the analysis. We determined the abundance of each species based on three periods of sampling during the rainy season (June, July and August 2009). The variation in species composition among plots was synthesized in two axes using Non-metric Multidimensional Scaling (NMDS) with the matrix of abundance and occurrence of the species. We used multiple regression analysis to test for variables that were capable of explaining the variation in species composition. We found 3339 individuals, representing 19 species and 5 families. Most species were found at the beginning, and most individuals were found in the middle of the rainy season. *Dendrosophus* sp. was the most abundant species, and *Osteocephalus* aff. *taurinus* was the least abundant. *Dendropsophus* sp., *Hypsiiboas* sp., and *Leptodactylus* aff. *andreae* accounted for 63.8% of all individuals found in the plots. The first and second axes of the NMDS organized the plots along the gradient of soil clay content. Canopy openness, herb cover, soil sand content, slope and number of trees on the plots were correlated with soil clay content and, therefore, also explained the variation in the assemblage composition. Considering only the plots subject to flooding, soil clay content was also the major environmental factor, leading to important habitat heterogeneity, responsible for the anuran assemblage structure in the Viruá National Park. The results are not only of ecological interest but also of practical significance for the conservation of anurans in flooded tropical forests.

Key words: Anura, flooded forest, distribution patterns, environmental gradients, Northern Amazonia.

SUMÁRIO

AGRADECIMENTOS.....	v
RESUMO.....	vi
ABSTRACT.....	vii
LISTA DE FIGURAS.....	ix
INTRODUÇÃO GERAL.....	x
ARTIGO.....	1
ABSTRACT.....	2
INTRODUÇÃO.....	3
MATERIAL E MÉTODOS.....	5
RESULTADOS.....	11
DISCUSSÃO.....	13
CONCLUSÕES GERAIS.....	42
REFERÊNCIAS BIBLIOGRÁFICAS.....	43
ANEXO A-ATA AULA QUALIFICAÇÃO	57
ANEXO B- FICHAS DE AVALIAÇÃO DA BANCA NÃO PRESENCIAL	58
ANEXO C-ATA DEFESA PRESENCIAL.....	61

LISTA DE FIGURAS

FIGURE 1. Location of the study area and map of the 5x5-km trail grid of the Viruá National Park (Roraima state, Brazil), highlighting the location of the 30 sampling plots (solid rhombus). Modified version from <http://ppbio.inpa.gov.br/>

FIGURE 2. Rarefaction curves based on the number of plots (A) and the number of individual anurans (B) for each sampling period (not including species sampled only occasionally). The first sampling occasion (June) corresponds to the beginning of the rainy season, the second sampling occasion (July) corresponds to the middle of the rainy season and the third sampling occasion (August) corresponds to the end of the rainy season in PARNA Viruá. The continuous line is the average calculated with 1.000 randomizations and the dashed lines are the 95% confidence intervals.

FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordinations of sampling plots, based on (A) quantitative data and (B) qualitative data at PARNA Viruá. N= plots located in non flooded areas, F= plots located in seasonally flooded forest areas, C= plots located in seasonally flooded campina areas. Blue lines combine group items to their centroids representing the cluster of the plot's ordinate by type of habitat structure.

FIGURE 4. Distribution of anuran species abundance along the soil clay content gradient in the study plots at PARNA Viruá.

FIGURE 5. Nonmetric multidimensional scaling (NMDS) ordination of plots, based on Bray Curtis dissimilarities, showing differences in anuran species assemblages in relation to environmental variables. Open triangles indicate plots of seasonally flooded terra firme, open circles represent non flooded terra firme plots and crosses represent seasonally flooded campina plots. Arrows are significant correlations of environmental variables (plot altitude and plot soil clay and silt content) with NMDS axes. The length of the arrows increases with correlation coefficients and points to the direction of most rapid change in the environmental variable. Code name of the species according with table 2.

FIGURE 6. Partial regression of NMDS ordination values of qualitative data for anuran species composition on environmental predictor variables at PARNA Viruá, plot soil clay content (a), plot soil silt content (b) and plot altitude (c).

FIGURE 7. Partial regression of NMDS ordination values of quantitative data for anuran species composition on environmental predictor variables for seasonally flooded plots at PARNA Viruá, plot soil clay content (a), plot altitude (b) and plot water cover (c).

FIGURE 8. Partial regression of NMDS ordination values of qualitative data for anuran species composition on environmental predictor variables for seasonally flooded plots at PARNA Viruá (plot soil clay content (a), plot altitude (b) and plot water cover (c)).

INTRODUÇÃO GERAL

Condições climáticas favoráveis de umidade e a precipitação permitiram o desenvolvimento de altos níveis de diversidade de anuros na Amazônia (Hero 1990, Zimmerman & Rodrigues 1990, Duellman 1995, Lima *et al.* 2006), assim como uma alta diversidade de modos reprodutivos (Hödl 1990). Apesar da diversidade conhecida, a informação sobre a diversidade de anuros na Amazônia é ainda fragmentada, especialmente no que se refere à composição de espécies em assembléias. Os dados disponíveis indicam que existe alta variabilidade na composição de assembléias de anfíbios em escala regional na Amazônia (Azevedo-Ramos & Galatti 2002), e os condicionantes históricos e ambientais que determinam os padrões de distribuição e co-ocorrência de espécies de anfíbios amazônicos ainda são pouco compreendidos (Duellman 1995, Menin *et al.* 2007).

Estudos sobre a ecologia de anuros realizados na Amazônia Central se concentraram basicamente em florestas de terra firme e enfocam temas como segregação dos sítios de vocalização (Hödl 1977), predação e os efeitos de parâmetros bióticos e ambientais na distribuição de girinos (Gascon 1991, Magnusson & Hero 1991, Hero *et al.* 1998, Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001, Rodrigues 2006, Neckel-Oliveira 2007) e os efeitos de impacto antrópico sobre populações e comunidades (Zimmerman & Bierregaard 1986, Tocher *et al.*, 1997, Tocher *et al.* 2001, Neckel-Oliveira & Gascon 2006). No entanto, poucos estudos trataram da relação entre fatores ambientais e assembléias de anuros tropicais e suas interações (Menin *et al.* 2007, Condrati 2009). Amostragens padronizadas de assembléias de anuros adultos realizados na Amazônia central encontram uma estreita relação das espécies com parâmetros específicos de seus habitats reprodutivos (Menin *et al.* 2007, Condrati 2009) como a disponibilidade de corpos de água e microhabitats terrestres com alta umidade (Aichinger 1987, Hödl 1990). No caso dos anuros com reprodução dependente de água, a quantidade, qualidade e distribuição de ambientes favoráveis são determinantes na estrutura das assembléias (Zimmermann & Bierregaard 1986, Gottsberger & Gruber 2004, Condrati 2009). Para espécies com reprodução terrestre, tanto os fatores topográficos quanto os edáficos, geram uma sutil distribuição diferencial mesmo que a maioria das espécies seja generalista, ocorrendo ao longo de toda a matriz da floresta (Menin *et al.* 2007).

Florestas sazonalmente inundáveis formam o segundo tipo de vegetação mais extenso na Amazônia. Situadas sobre topografia que favorece a inundação durante os períodos chuvosos (Prance 1980), elas formam habitats importantes para a reprodução de anuros. Assembléias de

anuros que habitam florestas sazonalmente alagáveis e os fatores que influenciam sua composição e distribuição são pouco conhecidos na Amazônia, mas alguns estudos sobre o tema foram realizadas em outras regiões do Brasil (Prado *et al.* 2005, Maltchik *et al.* 2008, Valerio-Brun 2008). Mudanças ambientais produzidas pelo alagamento poderiam resultar na variação da composição das assembléias (Hubbell 1979, Ernst & Rödel 2006), devido à estreita dependência da reprodução dos anuros com a precipitação (Crump 1974, Bastazani *et al.* 2007) e a fidelidade dos anuros a seus habitats reprodutivos (Zimmerman & Bierregaard 1986).

Variáveis ambientais como a precipitação e o hidroperíodo estão associados com a ocorrência e distribuição das espécies, afetando o tempo de reprodução e a duração do período reprodutivo de anuros tropicais (Duellman 1988, Semlitsch *et al.* 1996, Wellborn *et al.* 1996, Gottsberger & Gruber 2004). A atividade reprodutiva de anuros em áreas tropicais é intensa na época de chuvas (Aichinger 1987, Abrunhosa *et al.* 2006), e a abundância total de indivíduos está relacionada a estes breves períodos (Duellman 1995, Gottsberger & Gruber 2004). Diferenças na fenologia reprodutiva estão associadas ao modo reprodutivo das espécies e poderiam flutuar de acordo com as condições hidrológicas e a imprevisibilidade dos sítios reprodutivos (Gottsberger & Gruber 2004).

Estudos com assembléias de anfíbios indicam uma forte associação entre a composição de espécies e variáveis ambientais locais (Parris & McCarthy 1999, Parris 2004, Bastazani *et al.* 2007), ressaltando a relevância de variáveis ambientais locais como preditoras de assembléias de anuros (Menin 2005). Uma única variável ambiental (tamanho do igarapé ou o tipo de borda de poças, por exemplo) produz efeitos diferenciais na composição de anuros nas assembléias (Keller *et al.* 2009, Vasconcelos *et al.* 2009). Por outro lado, o enfoque e o tipo de análise dos padrões de composição de espécies deveriam se considerar independentemente, devido a que cada grupo funcional responde de maneira diferente às variáveis ambientais (Menin *et al.* 2007, Ernst & Rödel 2008, Keller *et al.* 2009). Para assembléias de anuros de serrapilheira e arbóreos, a variação na composição da assembléia explicada por parâmetros ambientais é de pouca importância devido a que os indivíduos podem se mover livremente na matriz de habitats inteiros e a que previsibilidade do ambiente foi unicamente detectada em habitats alterados por humanos (Menin *et al.* 2007, Ernst & Rödel 2005, Ernst & Rödel 2008). Em contraste, assembléias de anuros associados a áreas ripárias, onde a heterogeneidade ambiental, os efeitos espaciais e ambientes espacialmente estruturados são considerados relevantes (Keller *et al.* 2009,

Vasconcelos *et al.* 2009). Portanto, e especialmente devido à falta de conhecimento sobre a diversidade de anuros na Amazônia e sua relação com características do habitat, as projeções dos efeitos de variáveis preditoras em áreas pouco estudadas devem ser consideradas cuidadosamente. O efeito de variáveis ambientais na composição de espécies deve ser analisado separadamente para diferentes tipos de habitat (Vasconcelos *et al.* 2009).

Este estudo teve como objetivo, analisar os padrões de distribuição de assembléias de anuros em um gradiente de terra firme sujeito a diferentes períodos de alagamento. Esta heterogeneidade ambiental converte a área em um sítio ideal para estudar as variáveis ambientais que potencialmente podem estruturar assembléias de anuros. Realizamos amostragens padronizadas de anuros em 30 parcelas uniformemente distribuídas em uma área de 25 km², com o propósito de comparar a abundância de anuros e a composição de espécies entre parcelas sujeitas a diferentes períodos de alagamento. Nossas perguntas foram: i) a composição de anuros pode ser prevista em diferentes tipos de habitat?, ii) que variável ambiental pode influenciar a composição de espécies?; e iii) o período de alagamento é um importante preditor da composição de espécies de anuros na área?

1
2
3
4
5
6
7 Title: DISTRIBUTION PATTERNS OF ANURANS IN AN AREA OF 25KM² IN A
8 SEASONALLY FLOODED FOREST IN NORTHERN BRAZILIAN AMAZONIA
9
10

11 PAULA COCA SOTO^{1‡}, ALBERTINA P. LIMA², CLAUDIA KELLER³
12

13 ¹ *Graduate Program in Ecology, Instituto Nacional de Pesquisas da Amazônia – INPA Avenida*
14 *André Araujo 2969, 69011-970, Manaus, Amazonas, Brazil.*

15 ^{2,3} *Department of Ecology – CPEC, Instituto Nacional de Pesquisas da Amazônia – INPA,*
16 *Avenida André Araujo 2969, 69011-970, Manaus, Amazonas, Brazil.*
17

18 Running title: ANURANS ASSEMBLAGES IN FLOODED AMAZONIAN FOREST
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40

41 ([‡]) *Corresponding author*

42 *Mailing address: Instituto Nacional de Pesquisas da Amazônia – INPA, Avenida André Araujo 2969,*
43 *69011-970, Manaus, Amazonas, Brazil. Phone: +55-92- 36431816 , Fax: + 55-92-36431909.*

44 *E-mail: paulacoca@hotmail.com*
45
46

47 FORMATAÇÃO:

48 A dissertação apresentada segue as exigências do Art. 61 do Regimento Interno do Programa de Pós Graduação
49 em Ecologia do Instituto Nacional de Pesquisas da Amazônia, formatada segundo as normas do periódico
50 Austral Ecology.

51
52
53 **ABSTRACT**
54

55 Recent studies on arboreal and leaf litter anuran assemblages suggest that the variation in assemblage
56 composition explained by environmental parameters is only of minor importance. In contrast, anuran
57 assemblages of streams habitat heterogeneity, spatial effects and spatially structured environments
58 were considered relevant. Therefore, we investigated the patterns of distribution of anurans in an area
59 of 25 km² in a seasonally flooded forest situated in the Viruá National Park (Roraima state, Brazil) in
60 Northern Amazonia. We analyzed environmental variables potentially capable of predicting anuran
61 assemblage structure and composition in relation to environmental gradients in 30 plots evenly
62 distributed over a 5x5km area. Environmental variables with a significant effect in all plots were soil
63 texture and altitude. For plots subject to flooding we included water cover in the analysis. We
64 determined the abundance of each species based on three periods of sampling during the rainy season
65 (June, July and August 2009). The variation in species composition among plots was synthesized in
66 two axes using Non-metric Multidimensional Scaling (NMDS) with the matrix of abundance and
67 occurrence of the species. We used multiple regression analysis to test for variables that were capable
68 of explaining the variation in species composition. We found 3339 individuals, representing 19 species
69 and 5 families. Most species were found at the beginning, and most individuals were found in the
70 middle of the rainy season. *Dendrosophus* sp. was the most abundant species, and *Osteocephalus*
71 *taurinus* was the least abundant. *Dendrosophus* sp., *Hypsiobas* sp., and *Leptodactylus* aff. *andreae*
72 accounted for 63.8% of all individuals found in the plots. The first and second axes of the NMDS
73 organized the plots along the gradient of soil clay content. Canopy openness, herb cover, soil sand
74 content, slope and number of trees on the plots were correlated with soil clay content and, therefore,
75 also explained the variation in the assemblage composition. Considering only the plots subject to
76 flooding, soil clay content was also the major environmental factor, leading to important habitat
77 heterogeneity, responsible for the anuran assemblage structure in the Viruá National Park. The results
78 are not only of ecological interest but also of practical significance for the conservation of anurans in
79 flooded tropical forests.

80 *Key words:* Anura, flooded forest, distribution patterns, environmental gradients, Northern
81 Amazonia.
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101

INTRODUCTION

102
103
104 Favorable climatic conditions like humidity and rainfall have enabled the development of
105 high levels of anuran diversity in the Amazon (Hero 1990, Zimmerman & Rodrigues 1990,
106 Duellman 1995, Lima *et al.* 2006) as well as a high diversity of reproductive modes (Hödl 1990).
107 Despite the known diversity, information on amphibian diversity throughout the Amazon basin is
108 still fragmented, especially concerning species assemblage composition. Available data indicate a
109 high rate of turnover in amphibian assemblage composition throughout the region (Azevedo-
110 Ramos & Galatti 2002), which remains far from completely understood (Duellman 1995, Menin
111 *et al.* 2007).

112
113 Research on anuran ecology in Central Amazonia has been carried out mainly on terra
114 firme (non-flooded) rain forest, mostly regarding calling site segregation (Hödl 1977), predation
115 and the effects of biotic and environmental parameters on the distribution of tadpoles (Gascon
116 1991, Magnusson & Hero 1991, Hero *et al.* 1998, Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001,
117 Rodrigues 2006, Neckel-Oliveira 2007) and the effects of forest disturbance on populations and
118 communities (Zimmerman & Bierregaard 1986, Tocher *et al.*, 1997, Tocher *et al.* 2001, Neckel-
119 Oliveira & Gascon 2006). However, few studies have investigated the relationships between
120 environmental parameters and adult anuran assemblages (but see Menin *et al.* 2007, Condrati
121 2009). Standardized surveys conducted in central Amazonia on adult anuran assemblages describe
122 a tight association of species with specific breeding habitat parameters (Menin *et al.* 2007), such
123 as availability of water bodies and terrestrial microhabitats with high humidity (Aichinger 1987,
124 Hödl 1990). In the case of aquatic breeding anurans, the quantity, quality and distribution of
125 favorable environments are determinants of the assemblage structure (Zimmermann & Bierregard
126 1986, Gottsberger & Gruber 2004, Condrati 2009). For terrestrial breeding anurans, however,
127 topographic and edaphic parameters generate subtle differences in the distribution of species,
128 despite most species being habitat generalists and occurring in all kinds of forest matrix (Menin *et*
129 *al.* 2007).

130
131 Seasonally inundated forests comprise the second major vegetation type in the Amazon
132 where the particular topography favour inundation during each rainy season (Prance 1980)
133 forming important habitats for anuran reproduction. Anuran assemblages inhabiting these
134 seasonally flooded forests and the factors influencing their composition and distribution are
135 poorly known, however, a few studies on anuran assemblages in flooded forest have been
136 undertaken in other regions of Brazil (Prado *et al.* 2005, Maltchik *et al.* 2008, Valerio-Brun

137 2008). Seasonal environmental changes induced driven by flooding may result in variation in
138 community composition (Hubbell 1979, Ernst & Rödel 2006), because of the strict dependence of
139 anuran reproduction on rainfall (Crump 1974, Bastazani *et al.* 2007) and the fidelity of anurans to
140 their breeding habitat (Zimmerman & Bierregaard 1986).

141

142 Environmental variables such as rainfall and hydroperiod are associated with the
143 occurrence and distribution of species, affecting the timing of reproduction and the length of the
144 breeding season of tropical anurans (Wellborn *et al.* 1996, Semlitsch *et al.* 1996, Duellman 1988,
145 Gottsberger & Gruber 2004). Breeding activity in seasonal tropical sites is intense during the
146 rainy season (Aichinger 1987, Abruñhosa *et al.* 2006) and the overall abundance of anuran
147 individuals is closely related to these brief periods (Duellman 1995, Gottsberger & Gruber 2004).
148 Differences in reproductive phenology of species are associated with reproductive mode and may
149 fluctuate according to hydrological conditions and the unpredictability of breeding sites
150 (Gottsberger & Gruber 2004).

151

152 A number of studies on amphibian assemblages indicate strong associations between
153 species composition and local environmental variables (Parris & McCarthy 1999, Parris 2004,
154 Bastazani *et al.* 2007), pointing out the relevance of local environmental variables as predictor of
155 anuran assemblages (Menin 2005). A single environmental variable, like stream size or the
156 number of edges types for example, has differential effects on different anuran assemblage
157 composition (Keller *et al.* 2009, Vasconcelos *et al.* 2009). Therefore different approaches and
158 kinds of analysis may be necessary to evaluate species composition patterns, because different
159 functional groups react differently to environmental variables (Menin *et al.* 2007, Ernst & Rödel
160 2008, Keller *et al.* 2009). For arboreal and leaf-litter anuran assemblages, the variation in
161 assemblage composition explained by environmental parameters is only of minor importance
162 because individuals can move freely across the entire habitat matrix and predictability by
163 environment was only detected in habitats altered by humans (Menin *et al.* 2007, Ernst & Rödel
164 2005, Ernst & Rödel 2008). In contrast, for stream-dwelling anuran assemblages habitat
165 heterogeneity, spatial effects and spatially structured environments were considered relevant
166 (Keller *et al.* 2009, Vasconcelos *et al.* 2009). Therefore, given our lack of knowledge of
167 Amazonian anuran diversity and its relation to habitat characteristics, the projection of the effect
168 of predictor-variables onto unstudied areas and habitats has to be considered very carefully. The
169 effect of environmental variables on species composition has to be analyzed separately for
170 different kinds of habitat (Vasconcelos *et al.* 2009).

171

172 In this study, we analyzed the distribution patterns of anuran assemblages in a gradient of
173 terra firme, forest subjected to different flooding periods. This environmental heterogeneity makes
174 the area an ideal site for studying environmental variables that potentially structure anuran
175 assemblages. We carried out standardized anuran surveys in 30 sampling plots evenly distributed
176 over a 25 km² area, in order to compare anuran abundance and species composition among plots
177 subject to different flooding hydroperiod. Our questions were: i) can anuran species composition
178 be predicted across different habitat types?; ii) what environmental variables are influencing
179 anuran species composition? ; and iii) is the flooding period an important environmental predictor
180 of anuran species composition in the area?

181

182

183

METHODS

184

Study area

185

186 The study area is located in the Viruá National Park, in the south of the state of Roraima, northern
187 Brazil (01°29'12" N, 61°02'52" W, 01°26'29" S e 61°00'08" E). The park covers an area of
188 227.000 ha and is bordered by the white-water Branco River and its tributary Anauá. The
189 vegetation is characterized by a transition between grass- and scrubland (*campina*), lower-canopy
190 and more open forest (*campinarana*), and higher-canopy, more dense and humid forest (*terra*
191 *firme* forest). The area is generally flat, with isolated rocky outcrops 45-130 m high, and a large
192 portion is subject to seasonal flooding. Forests are distributed along water bodies and on the
193 higher terrain. Mean annual rainfall is 1750 mm, and is concentrated in the rainy season, from
194 April to August, during which extensive areas may be flooded. A relatively extended dry season
195 occurs from September to March. Mean annual temperature is 32° C (Machado *et al.* 2004). The
196 seasonal flooding in the area is caused by direct rainfall and the overflow of small streams
197 crisscrossing the area, and the water capacity of the soil (Hamilton *et al.* 2000). Water from heavy
198 rainfall accumulates during the course of the wet season forming a network of small water bodies
199 that interconnect to form a floodplain system with water depth depending on local topography.
200 The superficial groundwater table and the presence of an impermeable organic layer in the soil act
201 as a physical barrier to water drainage, especially in flat terrains at lower altitudes (Schaefer *et al.*
202 2009).

202

203 Sampling was carried out on a 25-km² trail grid located in the northern portion of the park.
The grid encompasses all vegetation types described above. The grid consists of 6 5-km trails in

204 the east-west direction crossed perpendicularly by six 5-km trails in north-south direction,
205 arranged as a 5x5-km grid with 1x1-km resolution (Figure 1). Data were collected on 30 sampling
206 plots distributed at 1-km intervals along the east-west trails. Each plot is 250m-long and its central
207 line follows the altitudinal contour line of the starting point, in order to minimize soil variation
208 and, thus, within-plot environmental variability (Magnusson *et al.* 2005).

209

210 For analyses the sampling plots were treated separately as flooded and non flooded plots.
211 Of the 30 plots, 12 terra firme forest plots are never flooded, while the remaining plots (8 in terra
212 firme forest, 3 plots in campinarana forest and 7 in campina) are covered by water to varying
213 degrees during the yearly flooding season. Both campina and campinarana plots were considered
214 as belonging to one habitat category because both types of vegetation were present in most of
215 them, with a marked predominance of campina.

216

217 *Anuran survey*

218

219 Anurans were surveyed along the rainy season of 2009, from 10 June to 11 August. In
220 order to obtain a clear pattern of the temporal distribution of anurans, the surveys were divided
221 into three sampling occasion: (1)10-25 June, (2) 10-24 July, and (3) 30 July to 11 August. The
222 late start of the survey in relation to the normal start of the rainy season in mid April occurred
223 because of an unusual delay of the onset of rainfall in 2009, which started only at the beginning of
224 June. Anurans were sampled through the simultaneous use of VES (*visual encounter surveys*) and
225 -AES (*acoustic encounter surveys*) (Veith *et al.* 2004). Both methods are suitable for surveys
226 aiming at anuran species composition, richness and abundance (Crump & Scott 1994, Veith *et al.*
227 2004), for both short and long –term studies (Doan 2003), allowing to detect a great number of
228 individuals (Menin *et al.* 2008). The surveys were carried out at night by two observers (PCS and
229 a field technician). Two plots were sampled each night. The complete survey of all 30 plots lasted
230 at least 17 days because we did not survey during heavy rainfall episodes. Each plot was sampled
231 three times for about one hour between, 18:30 and 23:00. Species that vocalize in the evening
232 were also surveyed for about one hour between 16:30 and 18:30, such as *Leptodactylus* aff.
233 *andreae*, a diurnal litter-dwelling species.

234 Individuals were located visually or by their call. The observers walked following the
235 main axis of the plot, one behind the other, stopping and recording the number of vocalizing
236 individuals of each species and searching in the litter, trees and vegetation for anurans. For the

237 visual surveys we considered a maximal detection distance of 6 m on each side of the central line
238 of the plot. For the acoustic surveys the maximum detection distances varied according to the
239 species and the call intensity. For species that have a loud call, that may be heard more than 50-m
240 away (*Rhinella margaritifera*, *Hypsiboas crepitans*, *Hypsiboas multifasciatus*, *Hypsiboas* sp.,
241 *Scinax* aff. *garbei*, *Osteocephalus* aff. *taurinus*, *Leptodactylus* aff. *andreae* and *Leptodactylus*
242 *riveroi*), a maximal distance of 10-m was the recording limit for the acoustic surveys. For species
243 that vocalize in aggregations of more than 30 individuals (*Dendropsophus* sp., *Scinax*
244 *fuscomarginatus*, *Scinax ruber*, *Leptodactylus longirostris*, *Leptodactylus petersii*) the maximal
245 range for acoustic recording was 3-m distance, as it also was for species with low call intensity
246 (*Hypsiboas fasciatus*). A 3-m distance, allows to record a sharp and clean call. For each species,
247 the number of individuals recorded visually and acoustically was pooled. The maximal abundance
248 of each species per plot, based on the three sampling occasions, was used in the analyses.

249 All individuals were identified to species level. Individuals were captured if it was
250 necessary for identification. In order to form a reference collection of anurans for the Viruá
251 National Park, five individuals of each species were sacrificed using procainum hydrochloride,
252 preserved in 70% alcohol and deposited in the Amphibian and Reptile Collection of the Instituto
253 Nacional de Pesquisas da Amazônia (INPA-H). Species nomenclature followed Amphibian
254 Species of the World (Frost 2009).

255 *Environmental variables*

256
257 The following variables were measured for all plots during this study or were measured
258 previously by the Programa de Pesquisas em Biodiversidade- PPBio, and are available for all
259 users at <http://ppbio.inpa.gov.br/>, except water cover and water depth, which were estimated only
260 for plots with some degree of flooding during the study period.

261 Slope and altitude were measured for all plots in March and November 2006 respectively.
262 The altitude was obtained from direct field measurements by a professional surveyor. Slope was
263 defined as the mean value of six measures taken with a clinometer perpendicularly to the plot long
264 axis, at 50-m intervals (range= 0.0°- 24.8°).

265
266 Soil clay, silt and sand content were obtained from six soil samples per plot, taken at a
267 depth of 15 cm at the same points as for slope in November 2006. Samples for each plot were
268 combined, cleaned of roots, air-dried and sieved through a 2 mm sieve following Embrapa (1997)

269 methodology for determination of the percentage of clay, silt and sand of the soil. Analyses were
270 carried out at INPA's Soil and Plant Laboratory by MSc. Tânia Pimentel. Soil clay content varied
271 from 0.50-57.85 %, while soil silt content varied from 4.76-32.26% and sand content varied from
272 31.12-88.70%.

273

274 Number of trees and palm trees were counted in each plot between November 2006 and
275 July 2007, considering trees and palm trees with diameter at breast height (dbh)>1 cm.
276 Individuals with $dbh \geq 30$ cm were counted in an area of 1 ha (40 m x 250 m). Individuals with 10
277 $cm \leq dbh < 30$ cm were counted in an area of 250 x 20 m and individuals with $1 cm \leq dbh < 10$ cm
278 were counted in an area of 250 x 4-m.

279

280 Canopy openness in each plot was determined in December 2006 as an estimator of
281 environmental light availability or environmental light in each plot, i.e. the quantity of light that
282 actually strikes a point if there was no obstruction (leaves, branches, slope). Canopy cover was
283 measured using hemispherical photographs of the forest canopy. Photographs were taken with a
284 Nikon Coolpix digital camera 4500 and a hemispheric converter lens Nikon FC-E8
285 perpendicularly to the long axis of the plot at six points at 50-m intervals along the axis trail. The
286 photographs were analyzed with the GLA-Gap Light Analyzer software. The mean of the six
287 points was used as the percentage value of canopy cover for each plot.

288

289 Herb cover was sampled once during the first sampling occasion, using a modified version
290 of the point quadrat method (Bullock 1996), with 200 points per plot, spaced at 2-m intervals
291 along the plot long axis. A metallic rod was placed at each point, and the number of leaves and
292 branches that intersected the rod at 50 cm height was recorded. Percentage of herb cover for one
293 plot was obtained by summing up the number of records from all quadrat points and dividing the
294 result by the number of quadrat points (200) (range= 27.64-92.8%).

295

296 Litter depth was measured once during the first sampling occasion, at six points at 50-m
297 intervals along the plot long axis, using a metallic ruler. For the analysis we used the mean of the
298 six measurements to represent the litter depth (range= 2.98- 6.71 cm).

299

300 Water cover of flooded plots was recorded at 200 points per plot, at 2-m intervals along
301 the plot long axis. The presence-absence of water in each point was recorded and a percentage for
302 each sampling period was calculated dividing the number of positive records (points covered by

303 water) by the number of points (range= 13.91-95.5 %). Water depth was recorded with a metallic
304 ruler at six points, every 50-m along the plot long axis (range= 1.36-30.44 cm). Both water cover
305 and water depth were measured in each of the three sampling occasions (June, July and August)
306 and the mean of each variable was used in the analysis.

307

308

Assemblage analysis

309

310

311

312

313

314

315

316

We used sample and individual based rarefaction curves derived from 1000 randomizations of the original sampling order, without replacement, using EstimateS 8.2, Sobs Mao Tau index (Colwell *et al.* 2004, Colwell 2005) for all three sampling occasions. These curves enabled the evaluation of the number of plots and individuals necessary to reach the highest number of species in each sample (Menin *et al.* 2008).

317

318

319

320

321

322

323

324

325

326

327

Due to the fact that in studies with assemblages, each species represents a dimension in which plots may be ordered (Keller *et al.* 2009), an ordination technique is necessary to reduce dimensionality (McCune *et al.* 2002). We present separate analyses throughout using (1) abundance data, referred to as the quantitative analysis and (2) presence-absence data, referred to as the qualitative analysis. We performed the NMDS (Non-metric Multidimensional Scaling) to relate the community structure using the Bray-Curtis index as distance measurement for quantitative data and the Jaccard index for qualitative data (presence-absence) (NMDS; R package VEGAN, Oksanen *et al.* 2006). This technique is commonly regarded as the most robust and unconstrained ordination method in community ecology (Minchin 1987) and is well suited for ecological data, since it allows non-normal distributed and ranked variables (Kruskal 1964, Kenkel & Orloci 1986, McCune *et al.* 2002).

328

329

330

331

332

We performed two dimensional non metric multidimensional scaling (NMDS) using all sampling plots for both quantitative and qualitative data to evaluate the effect of habitat type on the anuran assemblages (R package VEGAN). MANOVA analysis was used to test for significant differences in assemblage structure among habitat types.

333

334

335

336

Pearson correlation was used to test for autocorrelation among environmental variables, which can bias the results of multiple regression analysis (Magnusson & Mourão 2005). Some of the environmental variables were strongly correlated (Table 1). The result of multiple regression

337 using clay content as a dependent variable showed a significant relation with number of trees ($t=$
338 $2.95, p=0.007$) and canopy cover ($t=-3.79, p=0.001$) but not with altitude ($t=1.75, p=0.093$). After
339 identifying intercorrelated variables and excluding them from further analyses, we used three
340 variables for multivariate regression: soil clay content, soil silt content and altitude. The three
341 variables were tested for spatial auto-correlation of independent variables using the Euclidean
342 Distance coefficient to calculate the geographic distance matrix and were not correlated with the
343 geographical distances among plots (Mantel test, $p = 0.15, p=0.24, p = 0.33$, respectively).

344

345 We used multiple regression to analyze the effect of environmental variables on anuran
346 species composition and we tested if environmental variables could structure the assemblages
347 along environmental gradients. The scores of the NMDS ordinations which represent the major
348 patterns in anuran assemblage composition were used as dependent variables in models of
349 univariate or multivariate regression. We used altitude, and soil clay and silt content as
350 independent variables in the regression model: Assemblage composition = $a + \text{altitude} + \text{soil clay}$
351 $\text{content} + \text{soil silt content}$.

352

353 The environmental variables (soil clay content, soil silt content, altitude) were fitted as
354 vectors to the NMDS ordination for quantitative data and we calculated the correlation
355 coefficients of environmental parameters with each of the ordination axes (Pearson's r) (Ernest &
356 Rödel 2006). Permutation tests were performed using the `envfit` function in the VEGAN package
357 (Oksanen *et al.* 2007).

358

359 To evaluate the effect of flooding on anuran assemblage composition, a NMDS ordination
360 for both quantitative and qualitative data was performed for flooded plots only. Finally, we used
361 multiple regression to relate the effect of flooding to species composition. We used the scores of
362 the NMDS ordinations as dependent variables in multiple regression models. We used plot
363 altitude, soil clay content and water cover as independent variables in the model: Assemblage
364 composition = $a + \text{plot altitude} + \text{soil clay content} + \text{water cover}$. We added the variable water
365 cover to our general model of multiple regression because it best represents the variation and
366 permanency of water in the plots. We did not include water depth in the analysis because it was
367 correlated with water cover (Pearson correlation $r = 0.65$) and we did not include soil silt content
368 because it was correlated with soil clay content (Pearson correlation $r = 0.56$).

369

370 All ordinations and analysis were made using the R package VEGAN (Oksanen *et al.*
371 2007) for R (R Development Core Team 2006).

372

373

RESULTS

374

375

Species richness and diversity

376

377 We recorded a total of 3339 individuals, representing 19 species and 5 families in 180
378 hours of plot sampling (Table 1). The composition of frog assemblages varied among plots.
379 *Dendropsophus sp.* was the most abundant species, and *Osteocephalus aff. taurinus* was the least
380 abundant. The three most abundant species in the grid area (*Dendropsophus sp.*, *Hypsiboas sp.*
381 and *Leptodactylus aff. andreae*) accounted for 63.8% of all frogs found in the plots.

382

383 Most of the species were nocturnal, only *Leptodactylus longirostris* and *Leptodactylus aff.*
384 *andreae* were found calling during the day. The calling activity of *Leptodactylus aff. andreae*
385 generally started at 15.30 and ended about 18.30, whereas *Leptodactylus longirostris* may extend
386 its activity over the first hours of the night.

387

388 *Dendropsophus sp.*, *Hypsiboas multifasciatus*, *Hypsiboas sp.*, *Scinax aff. garbei*,
389 *Leptodactylus aff. andreae* and *Leptodactylus petersii* were registered regularly in all three
390 sampling occasion. The number of species per plot and period varied from zero to six (mean= 2.4
391 \pm 1.65, N =90).The number of individuals found was higher on the first and second sampling
392 occasion and decreased in the third (Table 2).

393

394 With approximately 20 plots surveyed 85% of the species were sampled. However the
395 number of individuals necessary to sample the same percentage of species varied approximately
396 from 200 to 800 individuals (Figure 2).

397

398

Anuran species assemblages in relation to habitat types

399

400 The two dimensional ordination for the quantitative and qualitative data, explained,
401 respectively, 75 and 78 % of data variance. The correlation between the NMDS axes was not
402 significant ($r = 0.022$ and $r = -0.007$, respectively). Both ordination analyses indicated the presence
403 of distinct anuran assemblages in each of three habitat types surveyed (Figure 3). There was a

404 significant difference for both quantitative (Pillai trace=1.312; $F_{4-54}=25.74$; $p<0.001$) and
405 qualitative anuran species composition (Pillai trace=1.301; $F_{4-54}=25.126$; $p<0,001$), summarized by
406 the NMDS ordination among types of habitat.

407 *Effect of environmental variables on anuran species assemblages*

408 The two dimensional ordination of the NMDS for quantitative data used in multiple
409 regression indicated that species composition was related with soil clay content (Pillai
410 Trace=0.654; $F_{2-25}=23.67$; $p<0.00001$), soil silt content (Pillai Trace=0.3028; $F_{2-25}=5.428$;
411 $p<0.011$) and altitude (Pillai Trace=0.285; $F_{2-25}=4.97$; $p<0.015$). The distribution pattern of the
412 abundance of anuran species along the soil clay content gradient revealed a restricted distribution
413 related with flooding by type of habitat (Figure 4). There were species restricted to areas with less
414 soil clay content (associated with higher sand content), such as *Scinax* aff. *garbei*, *Leptodactylus*
415 *longirostris*, *Scinax fuscomarginatus*, *Hypsiboas crepitans* and *Hypsiboas* sp. Species such as
416 *Hypsiboas multifasciatus*, *Leptodactylus riveroi*, *Osteocephalus* aff. *taurinus*, *Scinax ruber*,
417 *Hypsiboas fasciatus*, *Dendropsophus* sp., *Leptodactylus pertersii* and *Rhinella margaritifera*
418 occurred in intermediate range within the clay gradient. *Leptodactylus* aff. *andreae* showed most
419 of its abundance restricted to high soil clay content plots, although it may also occur at
420 intermediate levels of clay content.

421

422 Using the environmental fitting to evaluate the relative importance of the predictor
423 variables, we calculated the correlation coefficients for the three environmental variables that
424 related significantly to species composition (soil clay content, soil silt content and altitude) with
425 each of the quantitative ordination axes. Soil clay content showed the highest and most significant
426 correlation with the ordinations (Table 3). Correlation with ordination axes was sufficiently strong
427 for the three environmental variables to enable graphical representation (Figure 5).

428 The qualitative ordination explained 77% of the variance in one dimension. The multiple
429 regression model explained 60% of the variance ($F_{3-26}= 15.79$; $p<0.0001$), soil clay content being
430 the most influential environmental variable ($t=-5.07$; $p<0.0001$). Soil silt content ($t=-1.805$;
431 $p=0.08$) and altitude ($t=-0.901$; $p=0.376$) had no influence on the qualitative composition of
432 anuran species assemblages. Partial regression for significant effects on predictor variables
433 showed a significant and negative effect of soil clay content (Figure 6a) and a non significant
434 effects for soil silt content (Figure 6b) and altitude (Figure 6c) on the qualitative composition of
435 anuran species.

436

437

438

439

440

441

442

443

444

445

446

447

448

449

450

451

452

453

454

455

456

457

458

459

460

461

462

463

464

465

466

467

468

469

470

Ordination of quantitative data of flooded plots with NMDS captured 57% of the variation in one dimension. There was evidence that the quantitative composition of the community was related only to plot soil clay content ($t = -4.639$; $p = 0.0003$). Plot altitude ($t = -1.064$; $p = 0.305$) and plot water cover ($t = -0.550$; $p = 0.591$) had no significant effect in the model. The model explained 62% of the variation in the quantitative composition of the assemblage ($F_{3-14} = 10.38$; $p = 0.0007$). Partial regression for significant effects of predictor variables showed a significant and negative effect of soil clay content (Figure 7a) and non significant effects of altitude (Figure 7b) and water cover (Figure 7c) on the anuran species quantitative composition.

Ordination of qualitative data of flooded plots with NMDS captured 83% of the variation in one dimension. The qualitative composition of the assemblage, represented by the ordination in one dimension, is related only to plot soil clay content ($t = -3.73$; $p = 0.002$), plot altitude ($t = -1.260$; $p = 0.228$) and plot water cover ($t = -0.908$; $p = 0.379$) had non significant effects on anuran species composition. The model explained about 62% of the variation in the qualitative composition of the assemblage ($F_{3-14} = 7.82$; $p = 0.002$).

Regression of the species composition ordination in one dimension for the tree environmental predictor variables (plot soil clay, plot altitude and plot water cover) was used to produce partial plots, showing the relationship of the dependent variable and the predictor variables. The plots illustrate the strong and positive effect of soil clay content (Figure 8a), and non significant effects of plot altitude (Figure 8b) and water cover (Figure 8c) on anuran species qualitative composition.

DISCUSSION

In this study we recorded 19 anuran species in the 25km² grid area, while 38 species have been registered in surveys encompassing other areas of the Viruá National Park (Gordo *et al.* 2009). These figures are much lower than other studies found in other areas of central Amazonia (Zimmerman & Simberloff 1996, Lima *et al.* 2006, Menin *et al.* 2008, Condrati 2009, Rojas 2010). Possibly this difference in anuran richness is explained by historical factors (Gascon 1990, 1991), differences in sampling effort among studies and/or differences in habitat type by the proximity to riparian areas (Menin *et al.* 2008, Condrati 2009, Rojas 2010).

471 As in Menin *et al.* (2008), Condrati (2009) and Rojas (2010) studies, we used
472 systematically distributed plots of 250 m length, allowing to survey efficiently all habitats
473 proportionally to their availability in the environment and estimate the abundance of many
474 species. Edaphic and vegetation characteristics may produce differences in species composition
475 and are considered important predictors of patterns of local diversity (Gascon *et al.* 2000, Menin
476 2005). Much of central Amazonia is covered by non-flooded terra-firme forests, which look
477 structurally homogeneous and generally contain relatively uniform forest (Costa *et al.* 2005). The
478 grid location in Viruá National Park encompasses patches of campina and campinarana within
479 terra firme forest. This high habitat heterogeneity and the presence of restricted-range species
480 (*Hyposiboas* sp., *Scinax* aff. *garbei*, *Dendropsophus* sp.) associated with scattered habitat patches
481 were not founded in other grid areas of the Programa de Pesquisas em Biodiversidade-PPBio in
482 Central Amazonia.

483

484 Different habitat types in the Viruá National Park sampling grid had marked differences in
485 richness and species composition. In particular, the campina plots subject to partial flood harbored
486 different species and had lower anuran diversity than the terra firme plots which harbored more
487 species that are also found in other terra-firme areas in central Amazonia (Lima *et al.* 2006, Menin
488 *et al.* 2008). In contrast, a study in south-eastern Perú, found that the floodplain forest exhibited
489 greater mean relative abundance of frogs than the terra firme forest, and the species richness was
490 also slightly higher in the floodplain forest than in terra firme forest (Von May & Donnelly
491 2009). The species with highest abundance in the study area were nocturnal and highly arboreal
492 (*Dendropsophus* sp. and *Hypsiboas* sp.). Only one diurnal terrestrial breeding species
493 (*Leptodactylus* aff. *andreae*) was found. *Dendropsophus* sp. was often associated with water
494 bodies and flooded areas (Faivovich *et al.* 2005), while *Hypsiboas* sp. was found exclusively in
495 open areas (*e.g.* campina areas or forest-edge) (Kok 2006, Kok & Kalamandeen 2008). Five
496 species were rare in the samples and were therefore not included in the analysis. The low
497 abundance recorded for these species could be due to inadequate survey methods (*e.g.* *Pipa pipa*),
498 asynchrony between calling activity of opportunistic breeders and the sampling period (*e.g.*
499 *Osteocephalus* sp.) or because the species were not homogeneously distributed over plots, and the
500 areas where it occurred predominantly were not sampled. For example, *Rhinella marina*,
501 *Physaleamus ephippifer* and *Leptodactylus knudseni* were found often in the grid trails, but not in
502 the plots, where they were found only occasionally.

503

504 We observed a temporal variation in levels of calling activity, abundance and occurrence
505 throughout the rainy season, as detected by other studies in tropical areas (Scott 1976, Allmon
506 1991, Duellman 1995, Vonesh 2001). For example, *Scinax ruber* was found only in the beginning
507 of the rainy season and *Leptodactylus* aff. *andreae* was more abundant in the beginning of the
508 rainy season. *Dendropsopus* sp., *Hypsiboas multifasciatus*, *Leptodactylus riveroi* showed a small
509 variation along the sample periods; and *Leptodactylus petersii* was more abundant at the end of
510 the rainy season. The majority of aquatic-breeding species showed great abundance in the middle
511 of the rainy season (*Hypsiboas fasciatus*, *Hypsiboas* sp., *Scinax* aff. *garbei*, *Leptodactylus*
512 *longirostris*). Our data show that different species have in general the same seasonal patterns of
513 abundance distribution in the rainy season (Aichinger 1987, Allmon 1991, Gottsberger & Gruber
514 2004), and the higher number of individuals was found in the middle of the rainy season as was
515 also reported in other studies (Duellman 1995, Menin *et al.* 2008, Condrati 2009, Rojas 2010),
516 and/or during peaks of heavy rainfall (Duellman 1995, Gottsberger & Gruber 2004).

517 The variation in the abundance of species during the rainy season is mainly related, to the
518 phenology of reproductive activity, environmental tolerances of individual species (Gardner *et al.*
519 2007b), the unique reproductive strategy to equal environmental restriction (Prado & Haddad
520 2005), the availability of reproductive sites (Valerio-Brun 2008) and the timing of calling
521 activity (Menin *et al.* 2008). This becomes very conspicuous at the end of the rainy season, when
522 there is a marked reduction in both the number of individuals and species found. In southern
523 Pantanal Brazil a similar decreasing of number of species was also found in the flooding season
524 because of the avoidance of aquatic predators for pressure on anuran eggs and larvae (Prado *et al.*
525 2005), and the highly rate of explosive breeders reproducing in the early rainy season (Prado *et al.*
526 2005, Valerio-Brun 2008). In flooded areas in France Morand & Joly (1995) found that floods of
527 short water duration influenced negatively amphibian richness. In contrast Maltchik *et al.* (2008)
528 found a strong resistance of amphibians to disturbance by floods because amphibian richness and
529 abundance did not change after floods, even for events of different durations.

530 *Leptodactylus* aff. *andreae*, a terrestrial breeding anuran, showed an abrupt drop in
531 abundance at the end of the rainy season, and was also the first species to vocalize in the area,
532 even before the start of the rainy season. Menin *et al.* (2007) showed the same pattern for
533 terrestrial breeding anurans in a non-flooded terra firme forest, in contrast with a seasonally
534 flooded forest in Guyana where terrestrial breeding anurans were continuously active with almost
535 no difference in calling activity between early, middle and late rainy season (Gottsberger &
536 Gruber 2004). The humid conditions could favour the terrestrial eggs, keeping them absent from

537 drier places (Giarretta *et al.* 1999) because the occurrence of these species are associated with
538 rainfall patterns (Gottsberger & Gruber 2004). *Leptodactylus longirostris* was found
539 predominantly in open areas (e.g campina) where males called from hidden position at the base of
540 grass. The species showed a higher abundance in the middle of the rainy season, like the nocturnal
541 species found in the area. In flooded Pantanal forest, more than two thirds of the species are
542 explosive breeders, reproducing in the early rainy season before insect and fish colonization
543 (Prado *et al.* 2005). Although we did not find overall many species of *Leptodactylus* genus in the
544 sampling occasions, it is likely that the increasing flood events in the grid area may be a limiting
545 factor restricting the presence of these species that build terrestrial foam nest which must be
546 exposed to partial flooding in order to enable aquatic larval development (Arzabe *et al.* 1998,
547 Arzabe 1999, Gottsberger & Gruber 2004, Prado *et al.* 2005, Von May & Donnelly 2009). In
548 general, they show a distinctive peak of activity at the beginning rainy season, and most of the
549 foam nests can be found only during the early rainy season (Gottsberger & Gruber 2004). It is
550 important that depending on the goals of the project (Doan 2003), the differences in reproductive
551 phenology among species should be taken into account in short-to-medium term monitoring
552 designs for anurans (Gardner *et al.* 2007b). Based in our results, we recommend that the middle of
553 the rainy season as the best sampling period for maximal species recording in Rapid Biological
554 Inventories (RAP).

555

556 In the Amazon local topography affects soil proprieties (Ranzani 1980, Chauvel *et al.*
557 1987, Becker *et al.* 1988, Costa *et al.* 2005), the dynamics of the forest (Castilho *et al.* 2006), the
558 composition of terrestrial herbs (Drucker *et al.* 2008), and the distribution of some anuran species
559 (Allmon 1991, Menin *et al.* 2007). Here, we have found a strong association between soil texture
560 and anuran assemblages. However, it is difficult to determine exactly if only the soil clay content
561 accounted for the observed differences in anuran assemblages in the study area, because
562 qualitative and quantitative species composition was also correlated with other environmental
563 variables. As the soil determines the architectural complexity of the forest (Laurence *et al.* 1999),
564 the different levels of heterogeneity and, consequently the amount of light penetrating reaching to
565 the forest floor (Vasconcelos *et al.* 2003), may indicate that part of the observed differences in
566 anurans assemblages is rather due to factors associated with soil type, such as vegetation structure
567 (Woinarski *et al.* 1999, Hillers *et al.* 2008), soil water drainage or arthropod prey availability
568 (Watling 2005). Therefore, edaphic characteristic could be considered an important predictor of
569 anuran assemblages in Amazonia (Gascon *et al.* 2000, Menin 2005, this study).

570

571 In spite of the fact that soil texture could influence indirectly the anurans composition in
572 tropical forests, rainfall is considered the primary factor triggering, controlling and regulating
573 breeding activity of anurans (Aichinger 1987, Allmon 1991, Duellman 1995, Bastazani *et al.*
574 2007) and is determinant for the seasonal variation in anuran community activity (Inger 1969,
575 Crump 1982, Gottsberger & Gruber 2004, Canavero *et al.* 2008). In flooded forests, is identified
576 as the principal cue promoting the anurans reproduction (Prado *et al.* 2005, Valerio-Brun 2008),
577 the intensity of rainfall in these areas, could favor also the availability of reproductive sites (Prado
578 *et al.* 2005, Valerio-Brun 2008) and promote the individual reproductive phenology (Gottsberger
579 & Gruber 2004) in different soil types (Watling 2005, this study). Hydroperiod fluctuation
580 depends on rainfall (Heyer *et al.* 1975, Semlitsch *et al.* 1996) and local topography (Prado *et al.*
581 2005, this study), changing rapidly the landscape and the availability of breeding sites. As 2009
582 rainfall was erratic and short during the breeding season, it could be an important factor
583 concerning the species living in such environments, affecting reproductive success, eggs and
584 larval survival (Heyer 1969).

585 The non-flooded terra firme plots generally had soil with higher clay content and are
586 located at higher altitudes. The soil of seasonally flooded terra firme plots had higher silt content
587 and the heterogeneity of species found in these plots was higher in contrast with the campina plots
588 where the sand content of the soil is higher and characterized by the presence of species restricted
589 to these habitat. Environmental structural variables as number of trees, canopy cover and herb
590 cover were correlated with soil clay content, showing indirectly a strong relation of anuran species
591 composition and vegetation structure. Vegetation complexity and heterogeneity are considered
592 important factors influencing species composition at local and regional scales (Parris & McCarthy
593 1999, Halverston *et al.* 2003, Parris 2004, Afonso & Eterovick 2007, Bastazani *et al.* 2007,
594 Vasconcelos *et al.* 2009), determining microhabitats, shelter, vocalization site and ovoposition
595 sites availability and diversity (Parris & McCarthy 1999, Afonso & Eterovick 2007).

596 Soil properties could influence the distribution of many amphibian species (Diller &
597 Wallace 1999, Dayton *et al.* 2004), soil humidity (Toft 1980, Giaretta *et al.* 1999, Bastazani *et al.*
598 2007) and soil pH (Wyman 1988). In Costa Rica Watling (2005) found a biased distribution of
599 anurans in two edaphically-differentiated forest types related to soil drainage. Breeding ponds in
600 southeastern Brazil showed that the main environmental descriptor determining the species
601 composition was the gradient of soil humidity in the margins of ponds which are important for the
602 calling activity (Vasconcelos *et al.* 2009), where soil moisture is a function of local differences in

603 soil texture (Becker *et al.* 1988). Woinarski *et al.* (1999) explain much of the variation in
604 Australian frog abundance by the association of landscape with soil type mostly at the margins of
605 seasonally inundated floodplains (clay soils). In central Amazonia in Reserva Ducke, where
606 habitat variation was subtle (Costa *et al.* 2005), terrestrial breeding anurans are mostly habitat
607 generalists, occurring across most of the edaphic gradients (Menin *et al.* 2007). In contrast, the
608 grid area of the Viruá National Park, encompasses part of all the habitat heterogeneity
609 characteristics of the park and the seasonal flooding leads to a differential occurrence of anurans
610 related mostly to their reproductive mode (Gottsberger & Gruber 2004) or related to particular
611 features of their habitat (Gascon 1991, Toledo *et al.* 2003, Ernst & Rödel 2006). The relatively
612 high structural habitat heterogeneity is likely to produce a great amount of microhabitats that can
613 be used by different species (Ernst & Rödel 2005, 2006) allowing to recognize different groups of
614 species, as was also observed for species associated to streams (Condrati 2009, Keller *et al.* 2009,
615 Rojas 2010).

616

617 Altitude was the third environmental feature determining the anuran composition in the
618 grid area. In general, areas with more soil clay content are areas at higher altitude and more
619 distant from streams (Chauvel *et al.* 1987) or flooded areas. The rate of flooding is also related to
620 topography, and may influence indirectly amphibian composition (Pearman 1997) because affect
621 the flood level and the water availability in the grid area. In central Amazonia, the apparent
622 relationship between altitude and species distribution could be a reflection of distance gradients to
623 the water bodies located at lower altitudes (Menin *et al.* 2007, Condrati 2009). In the sampling
624 grid of Viruá National Park, the lower areas are subject to seasonal flooding and the permanence
625 of water is related mostly to the pattern of rainfall, reaching higher flooding levels in the middle
626 of the rainy season. The hydrologic fluctuation in the grid area is also influenced by small streams
627 that increased the predator colonization, diversity and abundance in the flooded areas (Coca, pers.
628 obs.), specially a high density of fishes (J. do Vale *Personal Communication*) as was also
629 observed in flooded Pantanal forest (Prado *et al.* 2005). As was observed in other Amazonian
630 forest (Gascon 1991) stream habitats are unlikely sites for high anuran species richness for
631 constant predation pressure of fishes on tadpoles (Gascon 1989) having an influence on anuran
632 species occupancy and composition (Hero 1990, Azevedo-Ramos *et al.* 1999, Pazin *et al.* 2006).

633 Based on the three most important environmental features (soil clay content, soil silt
634 content and altitude), we were able to define two types of groups of breeding anurans: (a), an
635 unique specie that breed only in terrestrial environments, *Leptodactylus* aff. *andreae* that only use

636 the areas that never flood; (b) a group of species that inhabit areas of terra firme and campina that
637 are flooded in the rainy season. The physical features of the environment may prevent species
638 from colonizing certain sites (Eterovick & Barata 2006) and the pronounced heterogeneity
639 produced by seasonal flooding enhances habitat differentiation (availability of reproductive sites
640 and microhabitats), resulting in higher differentiation in anuran assemblages. The campina and
641 campinarana areas had their own restricted species, while the terra firme forest showed more
642 heterogeneity as it is defined by the flood pulse and the rainfall patterns in which water
643 permanency varied considerably. Climatic alteration of dry and rainy periods with the occurrence
644 of climatic events may produce alterations in developmental timing of some species, altering
645 phenology, reproduction and survivorship (Blaustein *et al.* 1994, Pounds & Crump 1994, Carey &
646 Alexander 2003, Lips *et al.* 2005, McMenamin *et al.* 2008).

647 The timing of inundation is another important variable for amphibian breeding sites
648 (Paton & Crouch 2002). In the study area, the seasonal flooding only reaches its peak in the
649 middle of the rainy season and the significant relationship of water cover and anuran species
650 composition in the flooded plots is a function of disturbances of flooding and drying. Flood events
651 occur with similar frequency in terra firme plots and campina plots after heavy rains, however,
652 flooding duration may have a greater influence on characteristics of anuran assemblages because
653 different anuran species show an association with a gradient of water body permanency related
654 with water volume (Skelly 1997). The campina plots are subject to short-term flooding as
655 compared to forested plots, because sandy soils are usually hydromorphic and the evaporation rate
656 is higher in the open campina areas. The terra firme forest plots provide suitable breeding habitats
657 for a greater range of species than campina plots, because they hold water for longer. The unstable
658 hydroperiod of breeding sites, especially during first rainfalls episodes, is a limiting factor,
659 restricting the presence of species that deposit their eggs directly in the water (Arzabe *et al.*
660 1998) and the limitation of these habitats may change throughout the season (Ernst & Rödel
661 2006). On the other hand, it is critical that ponds are flooded at the appropriate time to meet the
662 life history requirements of amphibian species that could potentially breed at the site (Semlitsch
663 1985, Pechmann *et al.* 1989, Paton & Crouch 2002). In general, for most hylids the proximity to
664 aquatic breeding habitat is relevant (Zimmerman & Bierregaard 1986) even if breeding conditions
665 persist also without heavy rainfall (Duellman 1995).

666 In general, the seasonal flooding and the short period of rainfall in Viruá National Park
667 may restrict anuran activity in the rainy season. The anuran species recorded showed a restricted

668 distribution that may reflect physiological constrains and habitat specialization (Ernst & Rödel
669 2006). The influence of seasonal flooding and accumulation of water in some of the plots during
670 the rainy season may avert terrestrial breeding species like *Leptodactylus* aff. *andreae*, that breed
671 instead in the higher dry areas, with moderated levels of humidity. Several studies have shown a
672 seasonal dispersal of litter frogs in the rainy season (Toft 1980, Rodriguez 1992, Giaretta *et al.*
673 1999), explosive reproduction generally in the early rainy period correlated with avoidance of
674 aquatic predators in the early rainy season (Prado *et al.* 2005) and a non homogeneous distribution
675 and abundance (Van Sluys *et al.* 2007) explained by local conditions such as humidity and depth
676 of the leaf litter (Toft 1980, Giaretta *et al.* 1997). Menin *et al.* (2007) suggested that terrestrial
677 breeding anurans occurred across most of the edaphic gradients showing a little beta diversity
678 largely due to subtle habitat variation among study sites in Central Amazonia. We disagree with
679 this generalization, the distribution pattern of *Leptodactylus* aff. *andreae* in the study area
680 responds to a variation in the availability of breeding sites as was suggested for Zimmerman &
681 Bierregaard (1986), consequently is not ascribe to seasonally flooded forest.

682
683

684 In fact, seasonal flooding, may have a positive influence in the aquatic breeding anurans
685 favoring the use of these areas in the reproductive period because soils with relatively high
686 available water capacity are likely important for the reproductive patterns of some species
687 (Bastazani *et al.* 2007), providing moist refuge sites or suitable water levels. Generally, the choice
688 of breeding sites by amphibians can be influenced by the quality of the surrounding terrestrial
689 habitat as well as by characteristics of the water body (Alford 1999, Semlitsch & Bodie 2003).

690
691
692

ACKNOWLEDGEMENTS

693 This work is a result of the masters thesis of PCS undertaken at the Instituto Nacional de
694 Pesquisas da Amazônia (INPA), supported by a fellowship from the Conselho Nacional de
695 Desenvolvimento Científico e Tecnológico (CNPq) and financial support and field infrastructure
696 provided by the Programa de Pesquisas em Biodiversidade- PPBio from the Brazilian Ministry of
697 Science and Technology. Specimens were collected under license #15338-2 from the Instituto
698 Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA); We thank T.
699 Pimentel for providing the soil data; A. Lisboa, B. Lisboa, I. Almeida and M. Costa for their
700 assistance in the Viruá National Park; O. da Silva for assistance in the field; V. Carvalho for aid in
701 taxonomic classification; F. Costa and V. Landeiro for reviewing earlier drafts; G. Coca helped

702 create the maps. We thank M. Menin, C. Prado and J. Watling for constructive and helpful
703 comments on the manuscript.

704

705

706

707

708

709

710

711

712

713

714

715

716

717

718

719

720

721

722

723

724

725

726

727

728

729

730

731

732

733

734

735

736

737

738

739

740

741

742

743

744

745

746

747

748

749

750

751

REFERENCES

- 752
753
754
755 Abrunhosa P., Wogel H.; Pombal J. (2006) Anuran temporal occupancy in a temporary pond from
756 the Atlantic rain forest, south-eastern Brazil. *Herpetological Journal* **16**, 115-122.
- 757 Afonso L.G. & Eterovick P. C. (2007) Spatial and temporal distribution of breeding anurans in
758 streams in southeastern Brazil. *Journal of Natural History* **41**, 949 – 963.
- 759 Aichinger M. (1987) Annual activity patterns of anurans in a seasonal Neotropical environment.
760 *Oecologia* **71**, 583-592.
- 761 Alford R. A. (1999) Ecology. Resource use, competition, and predation. In: *Tadpoles. The*
762 *Biology of Anuran Larvae* (eds R. W. McDiarmid & R. Altig) pp. 240–278. The
763 University of Chicago Press, Chicago, Illinois, U.S.A.
- 764 Allmon W. D. (1991) A plot study of forest floor litter frogs, central Amazon, Brazil. *Journal of*
765 *Tropical Ecology* **7**, 503–522.
- 766 Arzabe C., De Carvalho C. X. & Goes Costa M. A. (1998) Anuran assemblages in Crasto forest
767 ponds (Sergipe State, Brazil): comparative structure and calling activity patterns.
768 *Herpetological Journal* **8**, 111-113.
- 769 Arzabe C. (1999). Reproductive activity patterns of anurans in two different altitudinal sites
770 within the Brazilian Caatinga. *Revista brasileira de Zoologia* **16**: 851 – 864.
- 771 Azevedo-Ramos C., Magnusson W. E. & Bayliss P. (1999) Predation as the key factor structuring
772 tadpole assemblages in a savanna area in central Amazonia. *Copeia* **1999**, 22-33.
- 773 Azevedo-Ramos C. & Gallati U. (2002) Patterns of amphibian diversity in Brazilian Amazonia:
774 conservation implications. *Biological Conservation* **103**, 103–111.
- 775 Bastazani C. V., Munduruca J. F. V., Rocha P. L. B. & Napoli M. F. (2007) Which environmental
776 variables better explain changes in anuran community composition? A case study in the
777 Restinga of Mata de São João, Bahia, Brazil. *Herpetologica* **63**, 459-471.
- 778 Becker, P., Rabenold, P.E. , Idol J.R. & Smith A.P.(1988) Water potencial gradients for gaps and
779 slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* **4**,
780 173-184

- 781 Blaustein A., Wake D. & Sousa W. (1994) Amphibian declines: judging stability, persistence, and
782 susceptibility of populations to local and global extinctions. *Conservation Biology* **8**, 60-71.
- 783 Canavero, A., Arim M., Naya D.E., Camargo A., Rosa I. & Maneyro R. (2008) Calling activity
784 patterns in an anuran assemblage: the role of seasonal trends and weather determinants.
785 *North-Western Journal of Zoology* **4**: 29-41
- 786 Carey C. & Alexander M. (2003) Climate Change and amphibian declines: is there a link?
787 *Diversity and Distribution* **9**, 111-121.
- 788 Castilho C. V., Magnusson W. E., Araújo R. N. O., Luizão R. C. C., Luizão F. J., Lima A. P. &
789 Higuchi N. (2006) Variation in aboveground tree life biomass in a central Amazonian forest:
790 effects of soil and topography. *Forest Ecology and Management* **234**, 85–96.
- 791 Chauvel A., Lucas T. & Boulet R. (1987) On the genesis of the soil mantle of the region of
792 Manaus, Central Amazonia, Brazil. *Experientia* **43**, 234–241.
- 793 Condrati L.H. (2009) Padrões de distribuição e abundância de anuros em áreas ripárias e não
794 ripárias de floresta de terra firme na Reserva Biológica do Uatumã –Amazônia Central.
795 Dissertação de Mestrado, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas.
796 52 pp.
- 797 Colwell R. K. (2005) EstimateS: Statistical estimation of species richness and shared
798 species from samples. Version 7.5. User's Guide and application published at:
799 <http://purl.oclc.org/estimates>.
- 800 Colwell R. K., Mao C. X. & Chang J. (2004) Interpolating, extrapolating, and comparing
801 incidence-based species accumulation curves. *Ecology* **85**, 2717–2727.
- 802 Costa F. R. C., Magnusson W. E. & Luizão R. C. (2005) Mesoscale distribution patterns of
803 Amazonian understorey herbs in relation to topography, soil and watersheds. *Journal of*
804 *Ecology* **93**, 863–878.
- 805 Crump M.L. & Scott Jr. N.J. (1994) Visual encounter surveys. In: *Measuring and Monitoring*
806 *Biological Diversity. Standard methods for amphibians*. (eds W.R. Heyer, M.A Donnelly.,
807 R.W. McDiarmid, L.-A.C.Hayek & M.S. Foster) pp. 84-92. Smithsonian Institution Press.
808 Washington, USA.

- 809 Crump, M. L. (1982) Amphibian reproductive ecology on the community level. In:
810 *Herpetological communities*. (ed. Scott Jr. N. J.) pp. 21-36. Wildlife Research Report 13,
811 Washington, USA.
- 812 Crump M. (1974) Reproductive strategies in tropical anuran community. *Miscellaneous*
813 *publication - University of Kansas, Museum of Natural History* **61**, University of Kansas,
814 Lawrence.
- 815 Dayton G. H., Jung R. E. & Droege S. (2004) Large-scale habitat associations of four desert
816 anurans in Big Bend National Park, Texas. *Journal of Herpetology* **38**, 619-627.
- 817 De Oliveira F.R & Eterovick P.C. (2009) The role of river longitudinal gradients, local and
818 regional attributes in shaping frog assemblages. *Acta Oecologica* **35**, 727-738.
- 819 Diller L. V. & Wallace R. L. (1999) Distribution and habitat of *Ascaphus truei* in streams on
820 managed, young growth forests in north coastal California. *Journal of Herpetology* **33**,71-79.
- 821 Doan T.M. (2003) Which methods are most effective for surveying rain forest herpetofauna?
822 *Journal of Herpetology* **37**, 72-81
- 823 Drucker D.P., Costa F. R. C. & Magnusson W. E. (2008) How wide is the riparian zone of small
824 streams in tropical forests? A test with terrestrial herbs. *Journal of Tropical Ecology* **24**, 65-
825 74.
- 826 Duellman W.E. (1995) Temporal fluctuations in abundances of anuran amphibians in a seasonal
827 Amazonian rainforest. *Journal of herpetology* **29**, 13-21.
- 828 Duellman W. E. (1988) Patterns of species diversity in anuran amphibians in the American
829 tropics. *Annals of the Missouri Botanical Garden* **75**, 79-104.
- 830 Ernst R. & Rödel M-O. (2008) Patterns of community composition in two tropical tree frog
831 assemblages: separating spatial structure and environment effects in disturbed and undisturbed
832 forests. *Journal of Tropical Ecology* **24**, 111-120.
- 833 Ernst R. & Rödel M-O. (2006) Community assembly and structure of tropical leaf-litter anurans.
834 *Ecotropica* **12**, 113-129.
- 835 Ernst R. & Rödel M-O. (2005) Anthropogenically induced changes of predictability in tropical
836 anuran assemblages. *Ecology* **86**, 3111-3118.

- 837 Eterovick P.C. & Barata I.M. (2006) Distribution of tadpoles within and among Brazilian streams:
838 the influence of predators, habitat size and heterogeneity. *Herpetologica* **62**, 365–377.
- 839 Faivovich J., Haddad C.F.B., Garcia P.C.A., Frost D.R., Campbell J.A. & Wheeler W.C. (2005)
840 Systematic review of the frog family Hylidae, with special reference to Hylinae: Phylogenetic
841 analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* **294**,
842 240 pp.
- 843 Frost, D. R. (2009) Amphibian species of the world: an online reference. Version 5.3. Electronic
844 database accessible at <http://research.amnh.org/vz/herpetology/amphibia/>. American Museum
845 of Natural History, New York, USA.
- 846 Gardner T. A., Ribeiro-Júnior M. A., Barlow J., Ávila-Pires T. A. S., Hoogmoed, M. & Peres C. A.
847 (2007a) The biodiversity value of primary, secondary and plantation forests for a Neotropical
848 herpetofauna. *Conservation Biology* **21**, 775–787.
- 849 Garner T.A. , Fitzherbet E.B, Drewes R.C., Howell K.M. & Caro T. (2007b) Spatial and temporal
850 patterns of abundance and diversity of an East African amphibian fauna. *Biotropica* **39**, 105-
851 113.
- 852 Gascon, C. 1989. Predator-prey size interaction in tropical ponds. *Revista Brasileira de Zoologia*
853 **6**:701-706.
- 854 Gascon C. (1991) Population- and community-level analyses of species occurrences of Central
855 Amazonian rainforest tadpoles. *Ecology* **72**, 1731–1746.
- 856 Giarretta A. A., Facure K. G., Sawaya R. J., Meyer J. H. De M. & Chemin N. (1999) Diversity
857 and abundance of litter frogs in a montane forest of Southeastern Brazil: seasonal and
858 altitudinal changes. *Biotropica* **31**, 669–674.
- 859 Gordo M., Carvalho V.T., Oliveira M.E., Esteves F.A.D., Lemos M., Bernhard R., Bernardes
860 V.C.D., Nascente L.B. & Seixas M. (2009) Diagnóstico Ambiental do Parque Nacional do
861 Viruá: Inventário de Herpetologia. Relatório Técnico. ICMBio.
- 862 Gottsberger B. & Gruber E. (2004) Temporal partitioning of reproductive activity in a neotropical
863 anuran community. *Journal of Tropical Ecology* **20**, 271–280.
- 864 Halverson M.A, Skelly D.K., Kiesecker J.M. & Freidenburg L.M. (2003) Forest mediated light
865 regime linked to amphibian distribution and performance. *Oecologia* **134**, 360-364.

- 866 Hamilton, S.K., Sippel, S.J. & Melack, J.M. (2002). Comparison of inundation patterns among
867 major South American floodplains. *Journal of Geophysical Research* **107** (D20), 8038.
- 868 Hero J.M. (1990) An illustrated key to tadpoles occurring in the Central Amazon rainforest,
869 Manaus, Amazonas, Brasil. *Amazoniana* **11**, 201-262.
- 870 Hero J.M., Magnusson W. E., Rocha C. F. D. & Catterall, C. P. (2001) Antipredator defenses
871 influence the distribution of amphibian prey species in the central Amazon rain forest.
872 *Biotropica* **33**, 131-141.
- 873 Hero J.M., Gascon C. & Magnusson, W.E. (1998) Direct and indirect effects of predation on
874 tadpole community structure in the Amazon rainforest. *Australian Journal of Ecology* **23**,
875 474-478.
- 876 Heyer W.R., McDiarmid R.W. & Weigmann D.L. (1975) Tadpoles, predation and pond habitats
877 in the tropics. *Biotropica* **7**, 100-111.
- 878 Heyer W.R. (1969) The adaptive ecology of groups of the genus *Leptodactylus* (Amphibia,
879 Leptodactylidae). *Evolution* **23**, 421-428.
- 880 Hillers A., Veith M., Rödel M-O. (2008) Effects of forest fragmentation and habitat degradation
881 on west african leaf-litter frogs. *Conservation Biology* **22**, 762-772.
- 882 Höld W. (1977) Call differences and calling site segregation in anuran species from Central
883 Amazonian floating meadows. *Oecologia* **28**, 351-363.
- 884 Höld W. (1990) Reproductive diversity in Amazonian lowland frogs. *Fortschritte der Zoologie*
885 **38**, 41-60.
- 886 Hubbel S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**,
887 1299-1309.
- 888 IBAMA (2008) Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis.
889 Disponível em: <<http://www.ibama.gov.br/siucweb/mostraUc.php?seqUc=113>>. Access in
890 June 25 2008.
- 891 Inger, R. F. (1969) Organization of communities of frogs along small rain forest stream in
892 Sarawak. *Journal of Animal Ecology* **38**, 123-148.

- 893 Keller A. M., Rödel E., Linsenmair E. & Grafe T. U. (2009) The importance of environmental
894 heterogeneity for species diversity and assemblages structure in Bornean stream frogs.
895 *Journal of Animal Ecology* **78**, 305-314.
- 896 Kenkel N.C. & Orloci L. (1986) Applying metric and nonmetric multidimensional scaling to
897 ecological studies: some new results. *Ecology* **67**, 919-928.
- 898 Kok P.J.R. (2006) A new species of *Hypsiboas* (Amphibia: Anura: Hylidae) from Kaieteur
899 National Park, eastern edge of the Pakaraima Mountains, Guyana. *Bulletin de l'Institut Royal*
900 *des Sciences Naturelles de Belgique, Biologie* **76**, 191-200.
- 901 Kok P.J.R. & Kalamandeen M. (2008) Introduction to the taxonomy of the amphibians of
902 Kaieteur National Park, Guyana. *Abc Taxa*, vol 5, i-ix, 278 p.
- 903 Kruskal J. (1964) Multidimensional scaling by optimizing goodness of fit to nonmetric
904 hypothesis. *Psychometrika* **29**, 1-27.
- 905 Laurance W.F., Fearnside P.M., Laurance S.G., Delamonica P., Lovejoy T.E., Rankin-de Merona
906 J., Chambers J.Q. & Gascon C. (1999) Relationship between soils and Amazon forest
907 biomass: A landscape-scale study. *Forest Ecology and Management* **118**, 127-138.
- 908 Lima A. P., Magnusson W. E., Menin M., Erdtmann L. K., Rodrigues D. J., Keller C. & Hödl W.
909 (2006) Guia de sapos da Reserva Adolpho Ducke, Amazônia Central. Atemma, Manaus. 168
910 p.
- 911 Lips K., Burrowes P., Mendelson III J. & Parra-Olea G. (2005) Amphibian population declines in
912 Latin America: a synthesis. *Biotropica* **37**, 222- 226.
- 913 Machado R. B., Aguiar L. M. S., Ramos-Neto M. B., Rodrigues F. H. G., Hass A. & Aquino F. G.
914 (2004) Atlas de Conservação da natureza brasileira – Unidades Federais. Metalivros. 335 p.
915 São Paulo.
- 916 Magnusson W. E., Mourão G. (2005) Estatística sem matemática. Editora Planta, Londrina. 138 p.
- 917 Magnusson W. E., Lima A. P., Luizão R., Luizão F., Costa F. R. C., Castilho C. V. & Kinupp V.
918 F. (2005) RAPELD: A modification of the Gentry method for biodiversity surveys in long-
919 term ecological research sites. *Biota neotropica* **5**, 1-6.

- 920 Magnusson W.E & Hero J.M. (1991) Predation and the evolution of complex ovoposition
921 behavior in Amazon rainforest frogs. *Oecologia* **86**, 310-318.
- 922 Maltchik L., Peixoto M.L, Sernet C., Moreira L.F.B. & Machado I.F. (2008) Dynamics of the
923 terrestrial amphibian assemblage in a flooded riparian Forest fragment in a neotropical region
924 in the south of Brazil. *Brazilian Journal Biology* **68**, 769-769.
- 925 McCune B., Grace J.B. & Urban D.L. (2002) Analysis of Ecological Communities. MjM
926 Software Design, Gleneden Beach, Oregon.
- 927 McMenamin S.K., Hadly E.A. & Wright C.K. (2008) Climatic change and wetland desiccation
928 cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy
929 of Sciences USA* **105**, 16988-16993.
- 930 Menin M. (2005) Padrões de distribuição e abundancia de anuros em 64km² de floresta de terra-
931 firme na Amazônia Central. Tese de doutorado, Instituto Nacional de Pesquisas da
932 Amazônia/Universidade Federal do Amazonas, Manaus, Amazonas. 103 pp.
- 933 Menin M., Lima A.P., Magnusson W. E. & Waldez F. (2007) Topographic and edaphic effects on
934 the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial
935 patterns. *Journal of Tropical Ecology* **23**, 539-547.
- 936 Menin M., Waldez F. & Lima A. P. (2008) Temporal variation in the abundance and number of
937 species of frogs in 10,000 ha of a Forest in Central Amazonia, Brazil. *South American
938 Journal of Herpetology* **3**, 68-81.
- 939 Minchin P.R. (1987) An evaluation of relative robustness of techniques for ecological
940 ordinations. *Vegetatio* **71**, 145-156.
- 941 Morand A. & Joly P. (1995) Habitat variability and space utilization by the amphibian
942 communities of the french Upper-Rhone floodplain. *Hydrobiologia* **301**: 249-257.
- 943 Neckel-Oliveira S. (2007) Effects of forest disturbance on breeding habitat availability for two
944 species of anurans in the Amazon. *Copeia* **2007**, 186–192.
- 945 Neckel-Oliveira S. & Gascon C. (2006) Abundance, body size and movement patterns of a
946 tropical treefrog in continuous and fragmented forests in the Brazilian Amazon. *Biological
947 conservation* **128**, 308-315.

- 948 Oksanen J., Kindt R., Legendre P. & O'Hara R.B. (2006) VEGAN: Community Ecology
949 Package. Available from URL: <http://cran.r-project.org>.
- 950 Paton P.W.C. & Crouch, W. B. (2002) Using the phenology of pond breeding amphibians
951 to develop conservation strategies. *Conservation Biology* 16, 194-204.
- 952 Parris K.M. & McCarthy M.A. (1999) What influences the structure of frog assemblages at forest
953 streams? *Australian Journal of Ecology* 24, 495-502.
- 954 Parris K.M. (2004) Environmental and spatial variables influence the composition of frog
955 assemblages in sub-tropical eastern Australia. *Ecograph* 27, 392-400.
- 956 Pazin V., Magnusson W.E., Zuanon J. & Mendonça, F. (2006) Fish assemblages in temporary
957 ponds adjacent to "terra firme" streams in Central Amazonia. *Freshwater Biology* 51, 1025-
958 1037.
- 959 Pearman P. B. (1997) Correlates of amphibian diversity in an altered landscape of Amazonian
960 Ecuador. *Conservation Biology* 11, 1211-1225.
- 961 Pechmann J. H. K., Scott D.E., Gibbons J.W. & Semlitsch R.D. (1989) Influence of wetland
962 hydroperiod on diversity and abundance of metamorphosing juvenile salamanders. *Wetlands*
963 *Ecology and Management* 1, 3-11.
- 964 Pounds A. & Crump M. (1994) Amphibian declines and climate disturbance: the case of the
965 golden toad and the harlequin frog. *Conservation Biology* 8, 72-85.
- 966 Prado C.P.A., Uetanabaro M. & Haddad C.F.B. 2005. Breeding activity patterns, reproductive
967 modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal,
968 Brazil. *Amphibia-Reptilia* 26, 211-221.
- 969 Prado C.P.A. & Haddad C.F.B. 2005. Size-fecundity relationships and reproductive investment in
970 female frogs in the Pantanal, South-Western Brazil. *Herpetological Journal* 15, 181-189.
- 971 Prance G.T. (1980) A terminologia dos tipos de florestas amazônicas sujeitas a inundação. *Acta*
972 *Amazonica* 10, 495-504.
- 973 R Development Core Team. (2006) R: A Language and Environment for Statistical
974 Computing. Available from URL: <http://cran.r-project.org>.

- 975 Rodriguez D. (2006) Influência de fatores bióticos e abióticos na distribuição temporal e
976 espacial de girinos de comunidades de poças temporárias em 64 km² de floresta de
977 terra firme na Amazônia central, Tese de doutorado, Instituto Nacional de Pesquisas da
978 Amazônia/Universidade Federal do Amazonas, Manaus, Amazonas. 100 pp.
- 979 Rodriguez L.O. (1992) Structure et organization du peuplement d'anoures de Cocha
980 Cashu, Parc National Manu. Amazonie Péruvienne. *Revue d'Ecologie la Terre et la*
981 *Vie* **47**, 151-197.
- 982 Rojas D. (2010) Distribuição e abundancia de anuros de florestas de terra firme na fazenda
983 experimental da Universidade Federal do Amazonas- Amazônia central, Tese de
984 mestrado Universidade Federal do Amazonas, Manaus, Amazonas. 60 pp.
- 985 Schaefer, C.E.G.R., Mendonça, B.A.F.& Fernandes-Filho, E. I. (2009) Geoambientes e
986 Paisagens do Parque Nacional do Viruá – RR: Esboço de Integração da
987 Geomorfologia, Climatologia, Solos, Hidrologia e Ecologia. Relatório Técnico.
988 ICMBio.
- 989 Semlitsch R. D. (1985) Analysis of climatic factors influencing migrations of the
990 salamander *Ambystoma talpoideum*. *Copeia* **1985**, 608–616.
- 991 Semlitsch R. D. & Bodie J.R. (2003) Biological criteria for buffer zones around wetlands
992 and riparian habitats for amphibian and reptiles. *Conservation Biology* **17**, 1219–1228.
- 993 Semlitsch R. D., Scott D. E., Pechmann J. H. K. & Gibbons, J. W. (1996) Structure and
994 dynamics of an amphibian community. In: *Long-term studies of vertebrate*
995 *communities* (eds M. L. Cody & J. A. Smallwood) pp. 217–247. Academic Press, New
996 York.
- 997 Skelly D.K. (1997) Tadpole communities. *American Scientist* **85**, 36.45.
- 998 Tocher M.D., Gascon C. & Meyer J. (2001) Community composition and breeding success
999 of Amazonian frogs in continuous forest and matrix habitat aquatic sites. In: *Lessons*
1000 *from Amazonia: the ecology and conservation of a fragmented forest* (eds R.O
1001 Bierregaard Jr, T.E Lovejoy & R.C.G Mesquita) pp. 235-247. Yale University Press,
1002 Connecticut, USA. p. 235-247.

- 1003 Toledo L.F., Zina J., & Haddad C.F.B. (2003) Distribuição espacial e temporal de uma
1004 comunidade de anfíbios anuros do Município de Rio Claro, São Paulo, Brasil. *Holos*
1005 *Environment* **3**, 136–149.
- 1006 Toft C.A. (1980) Seasonal variation in populations of Panamanian litter frogs in their prey:
1007 a comparison of wetter and drier sites. *Oecologia* **47**, 34-38.
- 1008 Urban D., Goslee S., Pierce K. & Lookingbill, T. (2002) Extending community ecology
1009 to landscapes. *Ecoscience* **9**, 200-202.
- 1010 Valerio-Brun L. (2008) Riqueza e abundância de anfíbios (Amphibia-Anura), Pantanal de
1011 Poconé, Município de Nossa Senhora do Livramento, Mato Grosso, Brasil. Dissertação
1012 de Mestrado, Universidade Federal de Mato Grosso/ Instituto de Biociências, Cuiabá,
1013 Mato Grosso. 83 p
- 1014 Van Sluys M., Vrcibradic D., Esbérad C.E.L., Alves M.A.S., Bergallo H.H. & Rocha
1015 C.F.D. (2007) Ecological parameters of the leaf litter frog community of an Atlantic
1016 Rainforest area at Ilha Grande, Rio de Janeiro State, Brazil. *Austral Ecology* **32**, 254-
1017 260.
- 1018 Vasconcelos H. L., Macedo, A. C. C. & Vilhena, J. M. S. (2003) Influence of topography
1019 on the distribution of ground-dwelling ants in an Amazonian forest. *Studies on*
1020 *Neotropical Fauna and Environment* **38**, 115–124.
- 1021 Vasconcelos T.S., Santos T.G., Rossa-Feres D.C. & Haddad C.F.B. (2009) Influence of the
1022 environmental heterogeneity of breeding ponds on anuran assemblages from
1023 southeastern Brazil. *Canadian Journal of Zoology* **87**, 699-707.
- 1024 Veith M., Lötters S., Andreone F. & Rödel M.-O. (2004) Measuring and monitoring
1025 amphibian diversity in tropical forests. II. Estimating species richness from
1026 standardized transect censusing. *Ecotropica* **10**, 85-99
- 1027 Von May R. & Donnelly M. A.. (2009) Do trails affect relative abundance estimates of
1028 rainforest frogs and lizards? *Austral Ecology* **34**, 613 – 620.
- 1029 Watling J. I. (2005) Edaphically-biased distributions of amphibians and reptiles in a
1030 lowland tropical rainforest. *Studies on Neotropical Fauna and Environment* **40**, 15–
1031 21.

- 1032 Wellborn G. A., Skelly D. K. & Werner, E. E. (1996) Mechanisms creating community
1033 structure across a freshwater habitat gradient. *Annual Review of Ecology, Evolution,*
1034 *and Systematics* **27**, 337-363.
- 1035 Woinarski, J.C.Z., Fisher A. & Milne D. (1999) Distribution patterns of vertebrates in
1036 relation to an extensive rainfall gradient and variation in soil texture in the tropical
1037 savannas of the Northern territory, Australia. *Journal of Tropical Ecology* **15**: 381-398.
- 1038 Wyman R. L. (1988) Soil acidity and moisture and the distribution of amphibians in five
1039 forests of Southcentral New York. *Copeia* **1988**, 394–399.
- 1040 Zimmerman B. L. & Rodrigues M. T. (1990) Frogs, snakes, and lizards of the INPA-WWF
1041 reserves near Manaus, Brazil, In: *Four Neotropical Rainforest* (ed. A. H. Gentry) pp.
1042 426-454, Yale University Press, New Haven.
- 1043 Zimmerman B. L. & Bierregaard R. O. (1986) Relevance of the equilibrium theory of
1044 island biogeography and species-area relations to conservation with a case from
1045 Amazonia. *Journal of Biogeography* **13**, 133–143.
- 1046 Zimmerman B.L. & Simberloff D. (1996) An historical interpretation of habitat use by
1047 frogs in a central Amazonian forest. *Journal of Biogeography* **23**, 27-46.
- 1048

TABLE 1. Pearson correlation among seven environmental variables measured in PARNA Viruá. Significant values are shown in bold. R is the Pearson correlation pairwise and P is the probability associated to the correlation.

		soil clay content	soil silt content	sand content	canopy openness	altitude	slope	herb cover
soil silt content	R	0.346						
	P	0.178						
soil sand content	R	-0.952	-0.472					
	P	<0.001	0.008					
canopy openness	R	-0.532	-0.355	0.587				
	P	0.002	0.054	0.0006				
altitude	R	0.451	0.289	-0.495	-0.214			
	P	0.012	0.121	0.005	0.257			
slope	R	0.540	0.372	-0.600	0.082	0.847		
	P	0.002	0.043	0.0005	-0.323	<0.001		
herb cover	R	-0.403	-0.134	0.403	0.582	-0.331	-0.316	
	P	0.027	0.480	0.027	0.0007	0.074	0.089	
number of trees	R	-0.322	0.136	0.250	-0.298	-0.196	-0.284	0.025
	P	0.101	0.499	0.209	0.131	0.326	0.151	0.902

TABLE 2. Number of plots in which each anuran species was recorded and number of individuals of each species recorded on each sampling occasion (1st, 2nd and 3rd) and overall (total) at PARNA Viruá. The total corresponds to the sum of the three samples. Habitat is indicated as N= non flooded plots, F= flooded plots, Fc= flooded plots situated in campina areas. Species code name next to the species.

Species (code)	Flood by type of habitat	No of Plots	Number of individuals			Total
			1st	2nd	3rd	
Bufonidae						
<i>Rhinella margaritifera</i> (Rhi.mar)	N,F	6	6	12	5	23
<i>Rhinella marina</i> (†)	N	1	–	1	–	1
Hylidae						
<i>Dendropsophus</i> sp. (Den.sp)	F,Fc	5	183	177	110	470
<i>Hypsiboas crepitans</i> (Hyp.cre)	Fc	2	14	44	4	62
<i>Hypsiboas fasciatus</i> (Hyp.fas)	F	4	3	41	22	66
<i>Hypsiboas multifasciatus</i> (Hyp.mul)	F,N,Fc	8	29	47	37	113
<i>Hypsiboas</i> sp. (Hyp.sp)	Fc,F,N	19	250	472	265	987
<i>Scinax fuscomarginatus</i> (Sci.fus)	Fc	6	67	44	6	117
<i>Scinax aff.garbei</i> (Sci.gar)	Fc	5	68	110	52	230
<i>Scinax ruber</i> (Sci.rub)	F	4	59	–	–	59
<i>Osteocephalus aff. taurinus</i> (Ost.tau)	N,Fc,F	5	6	1	2	9
<i>Osteocephalus</i> sp. (†)	N	1	1	–	–	1
Leiuperidae						
<i>Physalaemus ephippifer</i> (†)	N	1	–	1	–	1
Leptodactylidae						
<i>Leptodactylus aff.andreae</i> (Lep.and)	N,F,Fc	21	493	161	19	673
<i>Leptodactylus knudseni</i> (†)	N,F	2	1	1	–	2
<i>Leptodactylus longirostris</i> (Lep.lon)	Fc	6	88	153	45	286
<i>Leptodactylus petersii</i> (Lep.pet)	F,Fc,N	11	1	61	162	224
<i>Leptodactylus riveroi</i> (Lep.riv)	F,Fc	6	2	9	3	14
Pipidae						
<i>Pipa pipa</i> (†)	F	1	–	–	1	1
Total number of species			16	16	14	
Total number of individuals			1271	1335	733	3339

†= species occasionally sampled, not included neither in the rarefaction curves nor in the multivariate analysis

TABLE 3. Correlation of environmental variables with the anuran species assemblage ordination and ordination projection for each axis for quantitative assemblage data. Estimations of P values are based on 1000 permutations. Significant values for P are indicated with *.

environmental variable	NMDS1	NMDS2	r²	P
Soil clay content	-0.97515	0.22156	0.6761	<0.001 ***
Soil silt content	-0.57656	0.81705	0.2034	0.042 *
Plot altitude	-0.99242	-0.12289	0.2335	0.016 *

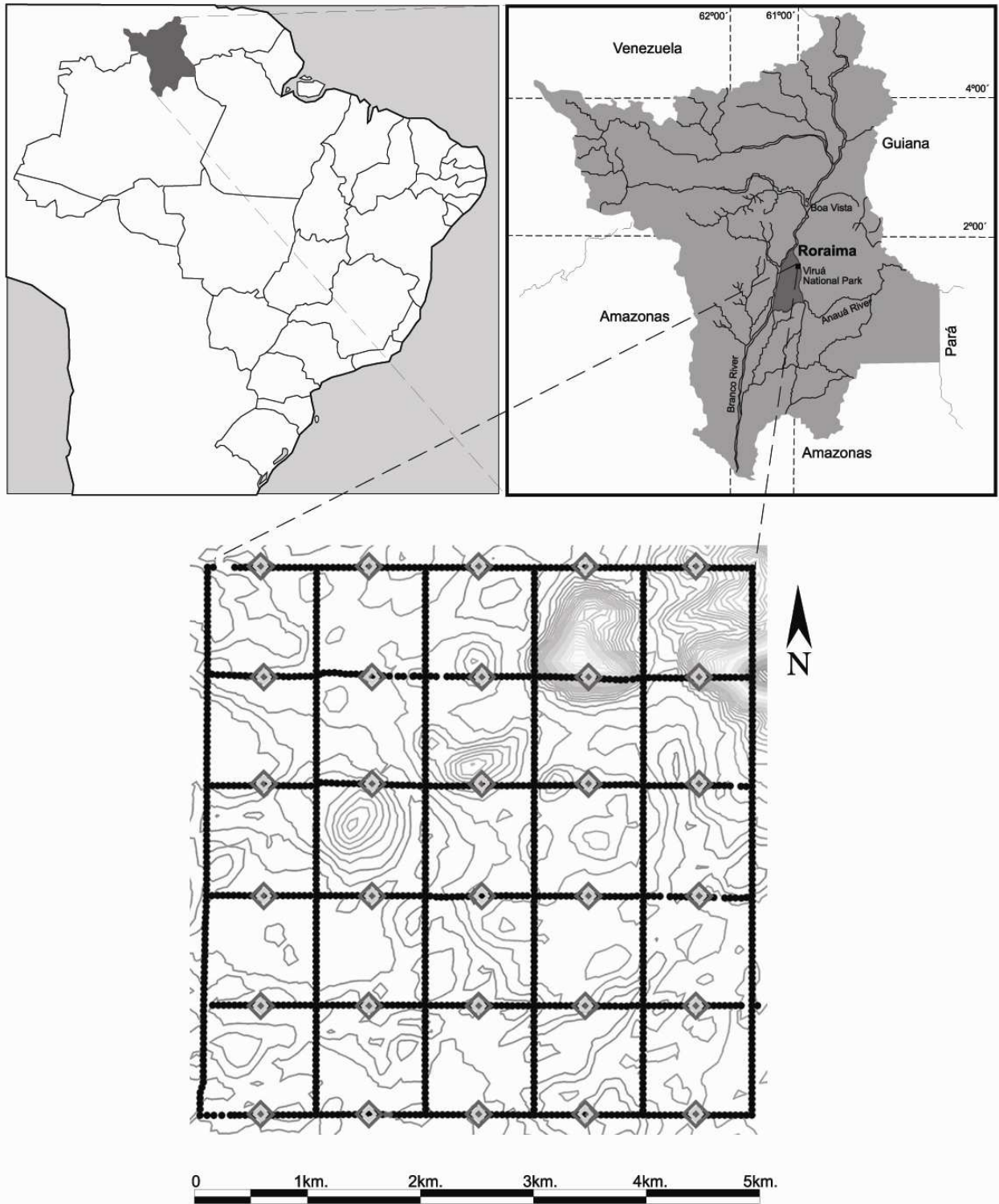


FIGURE 1. Location of the study area and map of the 5x5-km trail grid of the Viruá National Park (Roraima state, Brazil), highlighting the location of the 30 sampling plots (solid rhombus). Modified version from <http://ppbio.inpa.gov.br/>

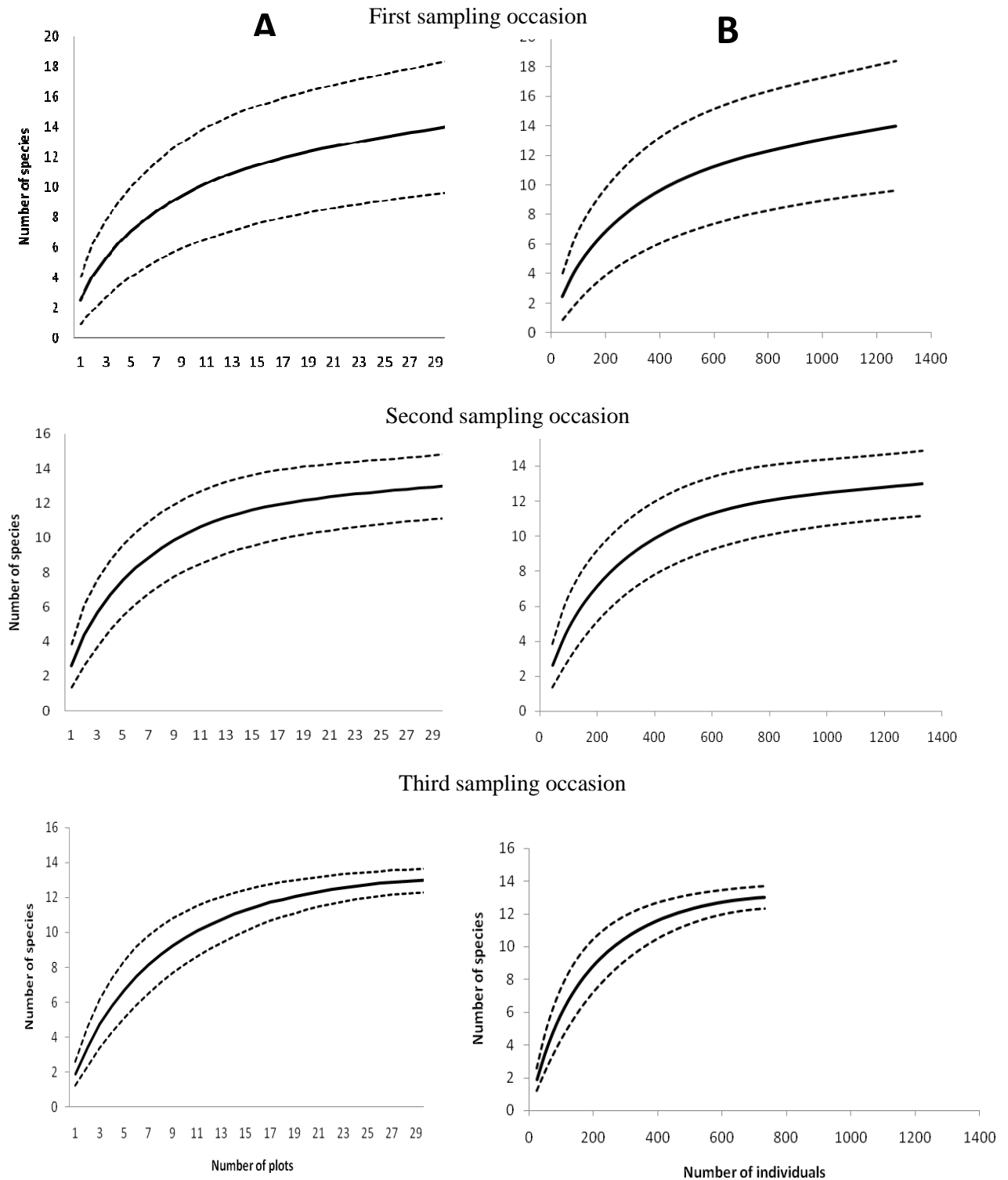


FIGURE 2. Rarefaction curves based on the number of plots (A) and the number of individual anurans (B) for each sampling period (not including species sampled only occasionally). The first sampling occasion (June) corresponds to the beginning of the rainy season, the second sampling occasion (July) corresponds to the middle of the rainy season and the third sampling occasion (August) corresponds to the end of the rainy season in PARNA Viruá. The continuous line is the average calculated with 1.000 randomizations and the dashed lines are the 95% confidence intervals.

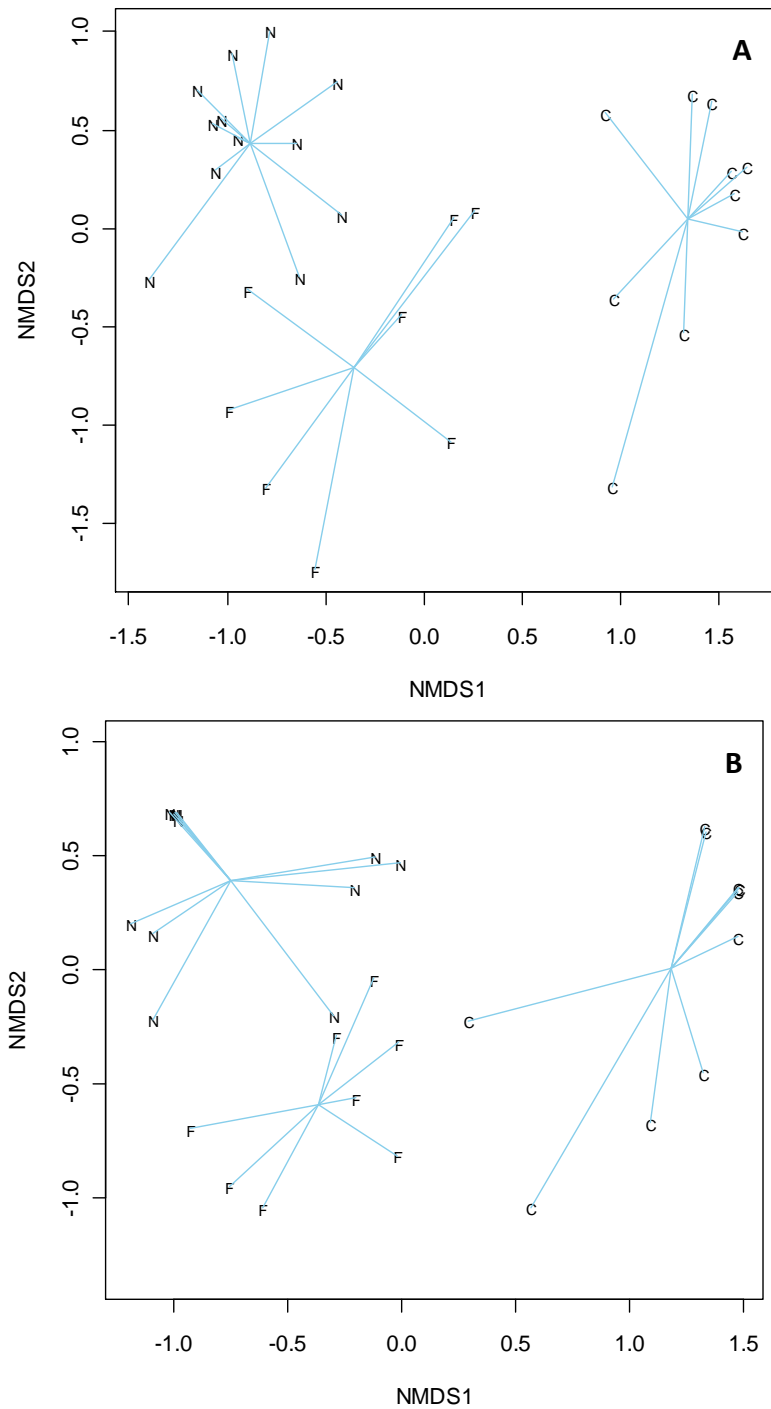


FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordinations of sampling plots, based on (A) quantitative data and (B) qualitative data at PARNA Viruá. N= plots located in non flooded areas, F= plots located in seasonally flooded forest areas, C= plots located in seasonally flooded campina areas. Blue lines combine group items to their centroids representing the cluster of the plot's ordinate by type of habitat structure.

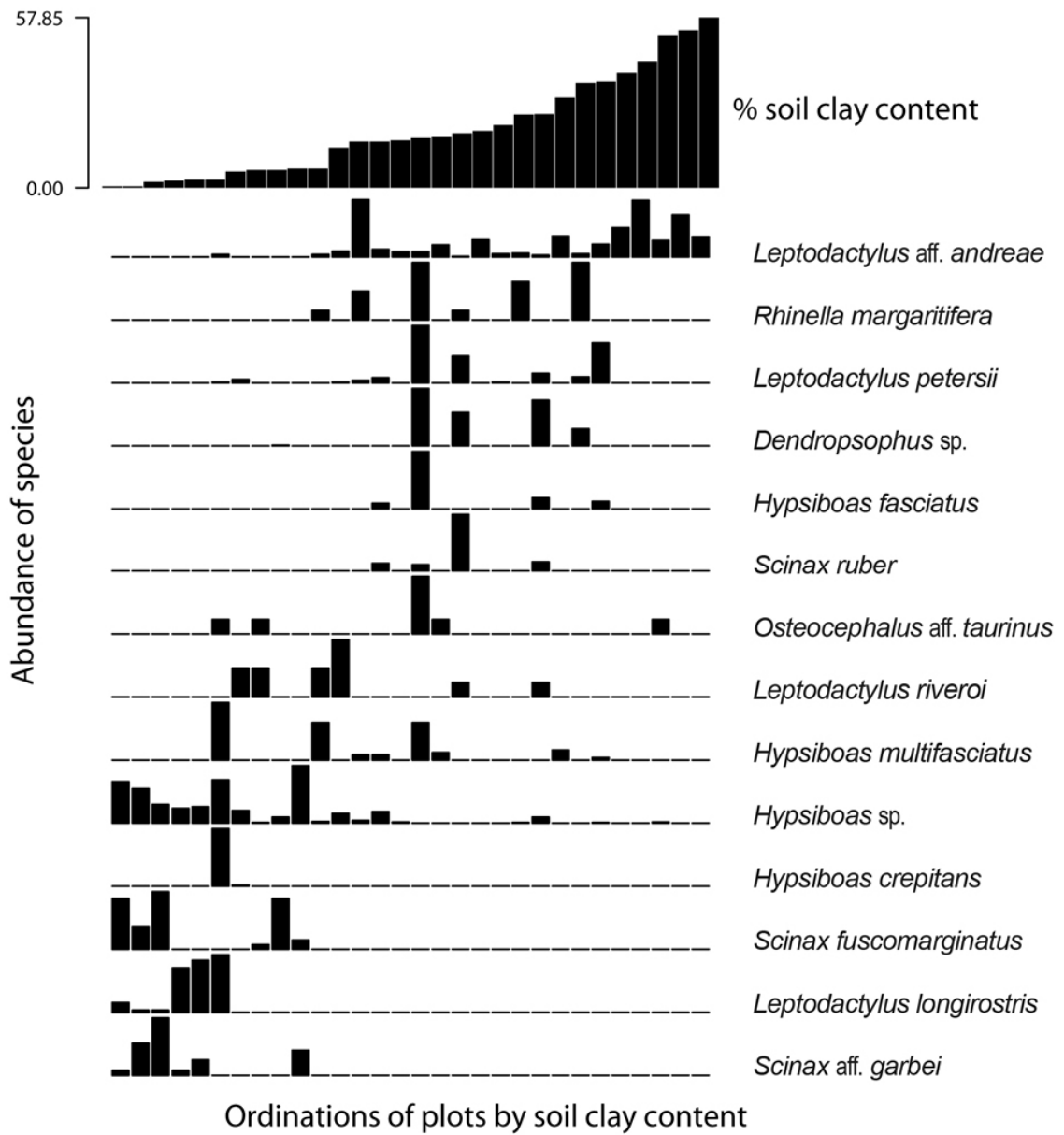


FIGURE 4. Distribution of anuran species abundance along the soil clay content gradient in the study plots at PARNA Viruá.

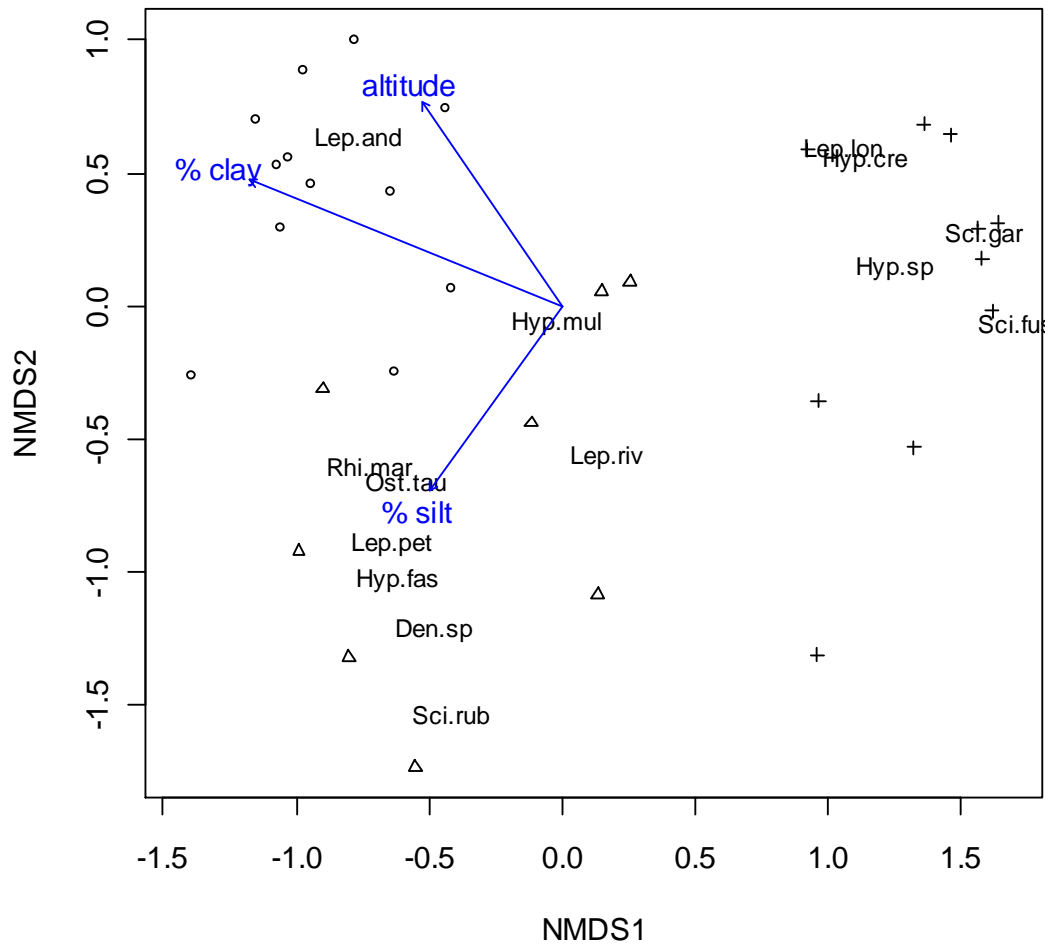


FIGURE 5. Nonmetric multidimensional scaling (NMDS) ordination of plots, based on Bray Curtis dissimilarities, showing differences in anuran species assemblages in relation to environmental variables. Open triangles indicate plots of seasonally flooded terra firme, open circles represent non flooded terra firme plots and crosses represent seasonally flooded campina plots. Arrows are significant correlations of environmental variables (plot altitude and plot soil clay and silt content) with NMDS axes. The length of the arrows increases with correlation coefficients and points to the direction of most rapid change in the environmental variable. Code name of the species according with table 2.

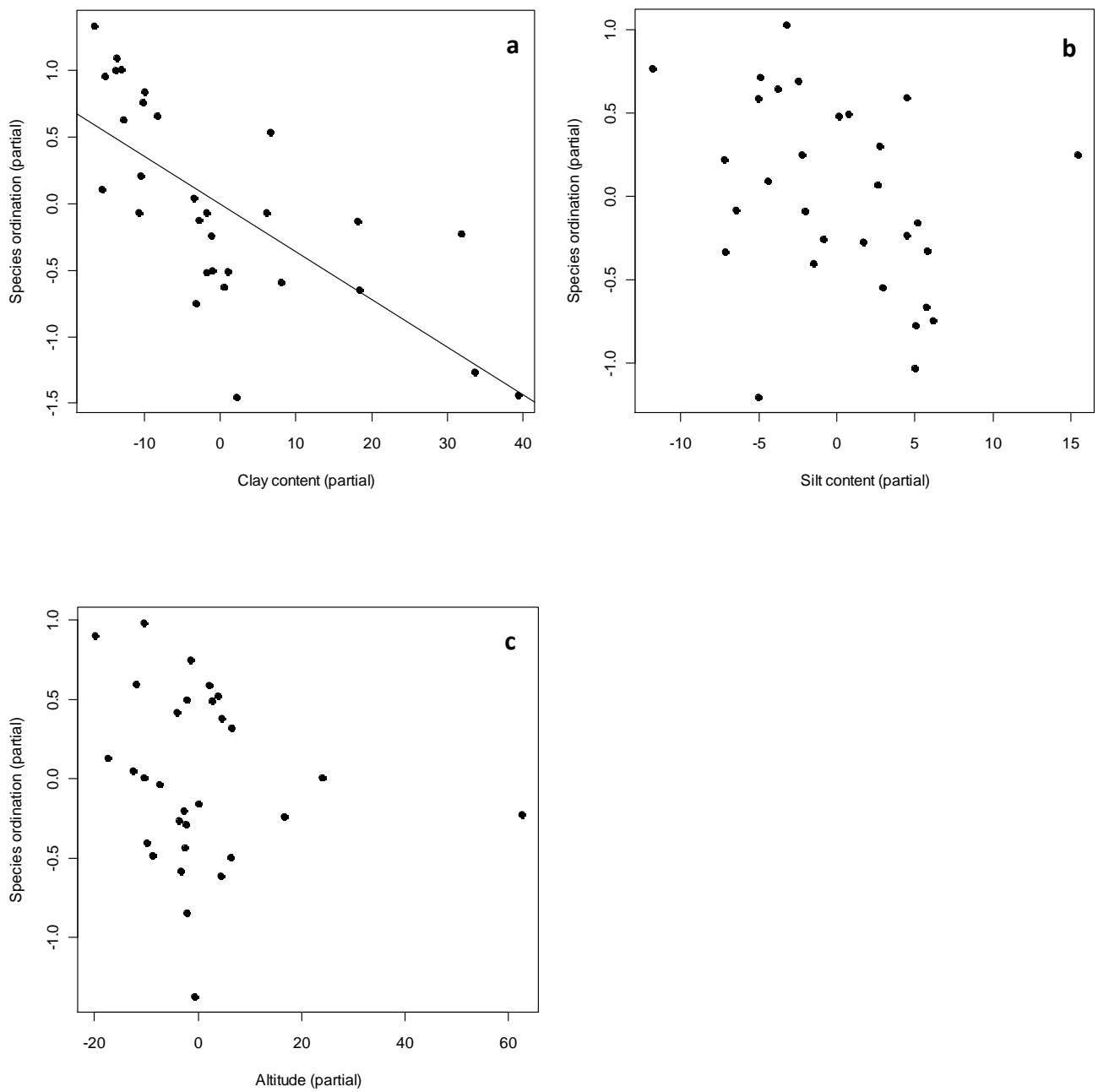


FIGURE 6. Partial regression of NMDS ordination values of qualitative data for anuran species composition on environmental predictor variables at PARNA Viruá, plot soil clay content (a), plot soil silt content (b) and plot altitude (c).

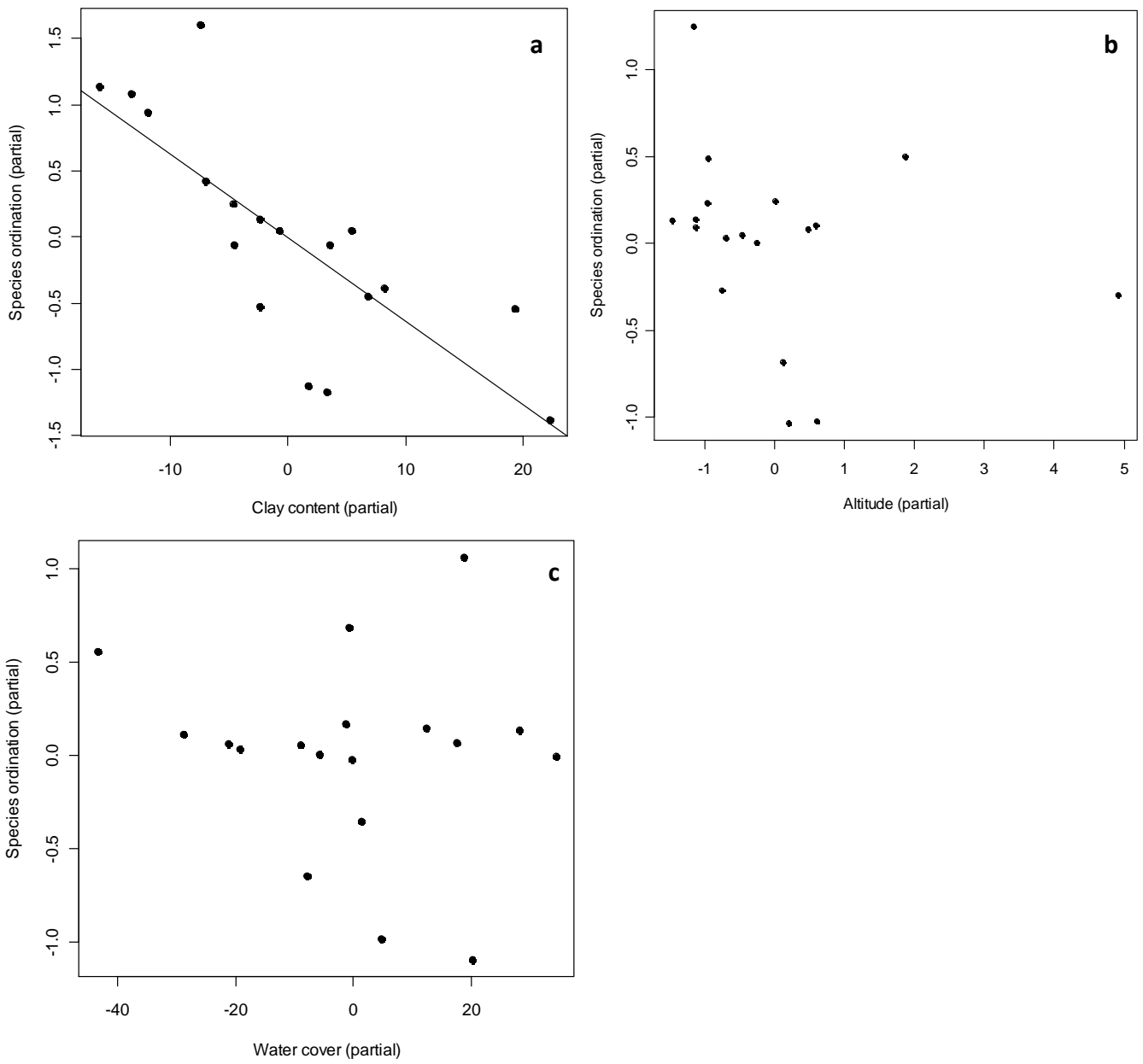


FIGURE 7. Partial regression of NMDS ordination values of quantitative data for anuran species composition on environmental predictor variables for seasonally flooded plots at PARNA Viruá, plot soil clay content (a), plot altitude (b) and plot water cover (c).

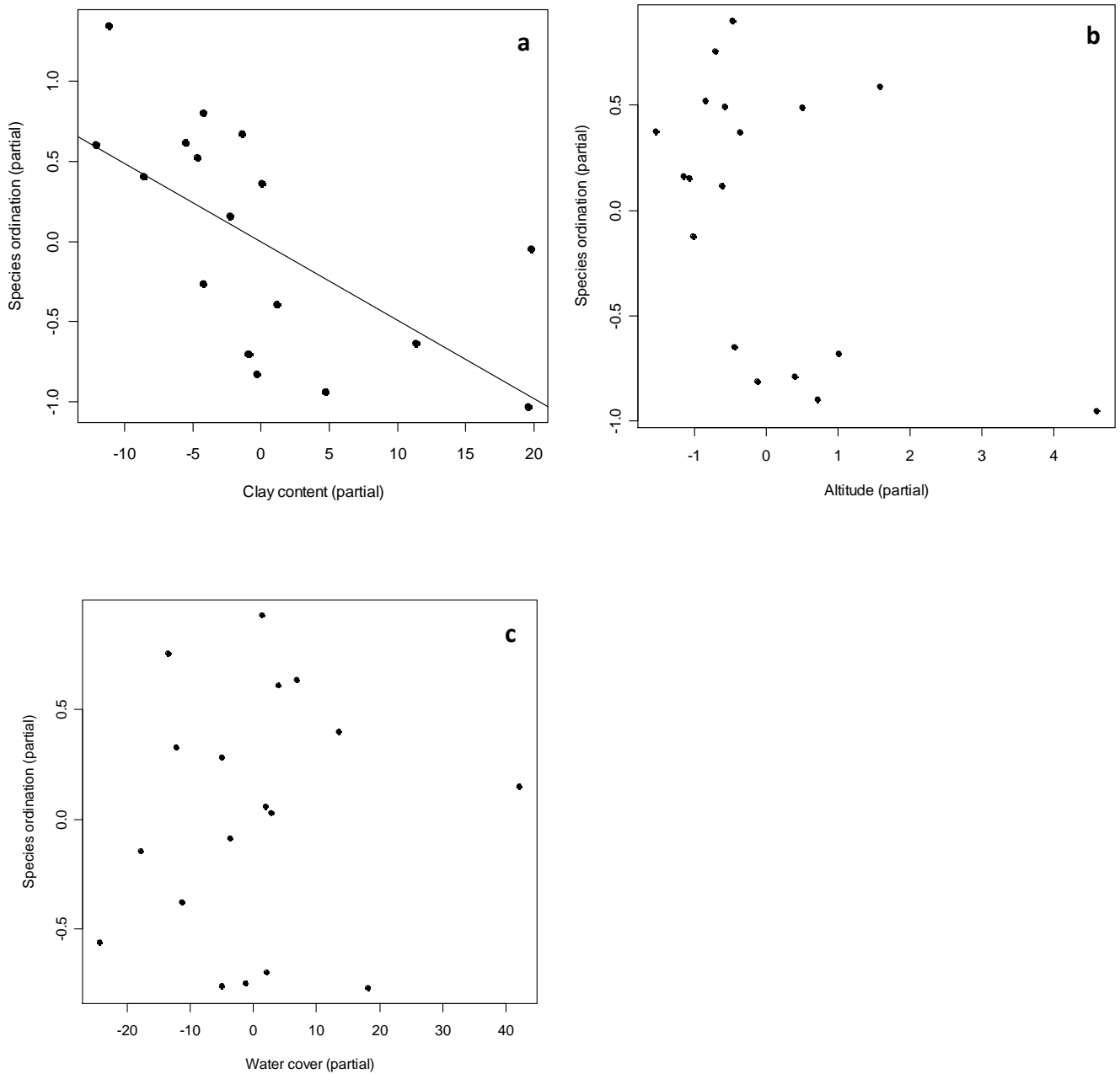


FIGURE 8. Partial regression of NMDS ordination values of qualitative data for anuran species composition on environmental predictor variables for seasonally flooded plots at PARNA Viruá (plot soil clay content (a), plot altitude (b) and plot water cover (c)).

APPENDIX 1. Pictures of representatives anurans in PARNA Viruá (left column) and their corresponding reproductive habitats (right column). (a) Leaf litter *Leptodactylus* aff. *andreae* of the non-flooded terra firme forest (b).(c) Arboreal *Dendropsophus* sp. and flooded terra firme forest (d).(e) Arboreal *Hypsiboas* sp. and campina area (f).



CONCLUSÕES GERAIS

Durante este estudo, realizado em 30 parcelas de amostragem distribuídas em uma área de 25km² floresta, campinarana e campina parcialmente alagáveis no Parque Nacional do Viruá no período chuvoso de 2009 (junho a agosto) foram registradas 19 espécies de anuros e um total de 3339 indivíduos pertencentes a cinco famílias: Bufonidae (10.52%), Hylidae (52.63%), Leiuperidae (5.26%), Leptodactylidae (26.32 %) e Pipidae (5.26%). A maioria dos indivíduos foi registrada no meio do período chuvoso.

A porcentagem de argila no solo, a porcentagem de silte no solo, a proporção de área alagável e a altitude das parcelas explicaram parte da variação na composição das espécies nas assembleias, mostrando que parcelas alagáveis apresentam número de espécies e composição de espécies diferentes nas parcelas não alagáveis.

Nossos resultados mostram uma forte relação dos anuros com seus habitats reprodutivos, determinada, por sua vez, com seu modo reprodutivo (Zimmerman & Bierregard 1986, Zimmerman & Simberloff 1996). Como já registrado em outros estudos (p.ex. Duellman 1995, Gottsberger & Gruber 2004) existiu uma possível correlação do padrão de atividade e abundância dos anuros no PARNA Viruá com o padrão de precipitação, que foi o principal fator desencadeador da atividade reprodutiva de anuros na área. A precipitação regula a flutuação hidrológica na floresta sazonalmente alagável provendo habitats desejáveis para a reprodução de anuros.

O forte efeito da composição do solo sobre a composição de assembleias de anuros reflete as restrições fisiológicas e a especialização de habitat das espécies de anuros (Ernst & Rödel 2006, Toledo *et al.* 2003) e é o resultado da associação da estrutura do solo com outros parâmetros ambientais relevantes para a ocorrência de anfíbios (Watling 2005).

A heterogeneidade ambiental da nossa área de amostragem de 25 km² no Parque Nacional do Viruá foi suficiente para detectar padrões de variação entre assembleias de anuros e sua associação com variáveis ambientais preditoras, como já foi demonstrado em estudos similares em outras áreas do mesmo tamanho (Menin *et al.* 2007, Condrati 2009). Nossos resultados indicam que fatores ambientais como textura do solo e a duração do hidroperíodo em áreas alagáveis, podem ser bons preditores da distribuição e composição de espécies de assembleias de anuros em ambientes amazônicos.

REFERÊNCIAS BIBLIOGRÁFICAS

- Abrunhosa P.; Wogel H.; Pombal J. 2006. Anuran temporal occupancy in a temporary pond from the Atlantic rain forest, south-eastern Brazil. *Herpetological Journal* 16, 115-122.
- Afonso L.G.; Eterovick P. C. 2007. Spatial and temporal distribution of breeding anurans in streams in southeastern Brazil. *Journal of Natural History* 41, 949 – 963.
- Aichinger M. 1987. Annual activity patterns of anurans in a seasonal Neotropical environment. *Oecologia* 71, 583-592.
- Alford R. A. 1999. Ecology. Resource use, competition, and predation, p. 240–278. In: McDiarmid, R.W; R. Altig, R. (Eds). *Tadpoles. The Biology of Anuran Larvae*. The University of Chicago Press, Chicago, Illinois, U.S.A.
- Allmon W. D. 1991. A plot study of forest floor litter frogs, central Amazon, Brazil. *Journal of Tropical Ecology* 7, 503–522.
- Arzabe C. 1999. Reproductive activity patterns of anurans in two different altitudinal sites within the Brazilian Caatinga. *Revista brasileira de Zoologia* 16: 851 – 864.
- Arzabe C.; De Carvalho C. X.; Goes Costa M. A. 1998. Anuran assemblages in Crasto forest ponds (Sergipe State, Brazil): comparative structure and calling activity patterns. *Herpetological Journal* 8, 111-113.
- Azevedo-Ramos C.; Magnusson W. E.; Bayliss P. 1999. Predation as the key factor structuring tadpole assemblages in a savanna area in central Amazonia. *Copeia* 1999, 22-33.
- Azevedo-Ramos C.; Gallati U. 2002. Patterns of amphibian diversity in Brazilian Amazonia: conservation implications. *Biological Conservation* 103, 103–111.
- Bastazani C. V.; Munduruca J. F. V.; Rocha P. L. B.; Napoli M. F. 2007. Which environmental variables better explain changes in anuran community composition? A case study in the Restinga of Mata de São João, Bahia, Brazil. *Herpetologica* 63, 459-471.
- Becker, P., Rabenold, P.E., Idol J.R. & Smith A.P. 1988 Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* 4, 173-184

- Blaustein A.; Wake D.; Sousa W. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8, 60-71.
- Canavero, A.; Arim M.; Naya D.E.; Camargo A.; Rosa I. ; Maneyro R. (2008) Calling activity patterns in an anuran assemblage: the role of seasonal trends and weather determinants. *North-Western Journal of Zoology* 4: 29-41
- Carey C.; Alexander M. 2003. Climate Change and amphibian declines: is there a link? *Diversity and Distribution* 9, 111-121.
- Castilho C. V.; Magnusson W. E.; Araújo R. N. O.; Luizão R. C. C.; Luizão F. J.; Lima A. P.; Higuchi N. 2006. Variation in aboveground tree life biomass in a central Amazonian forest: effects of soil and topography. *Forest Ecology and Management* 234, 85–96.
- Chauvel A., Lucas T.; Boulet R. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* 43, 234–241.
- Condrati L.H. 2009. *Padrões de distribuição e abundância de anuros em áreas ripárias e não ripárias de floresta de terra firme na Reserva Biológica do Uatumã –Amazônia Central*. Dissertação de Mestrado, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas. 52 pp.
- Colwell R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Colwell R. K.; Mao C. X.; Chang J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85, 2717-2727.
- Costa F. R. C.; Magnusson W. E.; Luizão R. C. 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *Journal of Ecology* 93, 863–878.
- Crump M.L.; Scott Jr. N.J. 1994. Visual encounter surveys, p. 84-92. In: Heyer, W.R; M.A Donnelly, M. A.; McDiarmid, R.W; Hayek, L.-A.C; Foster, M.S. (Eds). *Measuring and Monitoring Biological Diversity. Standard methods for amphibians*. Smithsonian Institution Press. Washington, USA.

- Crump, M. L. 1982 Amphibian reproductive ecology on the community level p. 21-36. In: Scott Jr. N. J. (Ed.) *Herpetological communities*. pp. 21-36. Wildlife Research Report 13, Washington, USA.
- Crump M. 1974. Reproductive strategies in tropical anuran community. *Miscellaneous publication - University of Kansas, Museum of Natural History* 61, University of Kansas, Lawrence.
- Dayton G. H.; Jung R. E.; Droege S. 2004. Large-scale habitat associations of four desert anurans in Big Bend National Park, Texas. *Journal of Herpetology* 38, 619-627.
- De Oliveira F.R; Eterovick P.C. 2009. The role of river longitudinal gradients, local and regional attributes in shaping frog assemblages. *Acta Oecologica* 35, 727-738.
- Diller L. V.; Wallace R. L. 1999. Distribution and habitat of *Ascaphus truei* in streams on managed, young growth forests in north coastal California. *Journal of Herpetology* 33, 71-79.
- Doan T.M. 2003. Which methods are most effective for surveying rain forest herpetofauna? *Journal of Herpetology* 37, 72-81
- Drucker D.P.; Costa F. R. C.; Magnusson W. E. (2008) How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. *Journal of Tropical Ecology* 24, 65-74.
- Duellman W.E. 1995. Temporal fluctuations in abundances of anuran amphibians in a seasonal Amazonian rainforest. *Journal of herpetology* 29, 13-21.
- Duellman W. E. 1988. Patterns of species diversity in anuran amphibians in the American tropics. *Annals of the Missouri Botanical Garden* 75, 79-104.
- Ernst R. & Rödel M-O. 2008. Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environment effects in disturbed and undisturbed forests. *Journal of Tropical Ecology* 24, 111-120.
- Ernst R. & Rödel M-O. 2006. Community assembly and structure of tropical leaf-litter anurans. *Ecotropica* 12, 113-129.
- Ernst R. & Rödel M-O. 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology* 86, 3111-3118.

- Eterovick P.C.; Barata I.M. 2006. Distribution of tadpoles within and among Brazilian streams: the influence of predators, habitat size and heterogeneity. *Herpetologica* 62, 365–377.
- Faivovich J.; Haddad C.F.B.; Garcia P.C.A.; Frost D.R.; Campbell J.A.; Wheeler W.C. 2005 Systematic review of the frog family Hylidae, with special reference to Hylinae: Phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* 294, 240 pp.
- Frost, D. R. 2009. Amphibian species of the world: an online reference. Version 5.3. Electronic database accessible at <http://research.amnh.org/vz/herpetology/amphibia/>. American Museum of Natural History, New York, USA.
- Gardner T. A.; Ribeiro-Júnior M. A.; Barlow J.; Ávila-Pires T. A. S.; Hoogmoed, M.; Peres C. A. 2007a. The biodiversity value of primary, secondary and plantation forests for a Neotropical herpetofauna. *Conservation Biology* 21, 775–787.
- Garner T.A.; Fitzherbet E.B; Drewes R.C.; Howell K.M.; Caro T. 2007b. Spatial and temporal patterns of abundance and diversity of an East African amphibian fauna. *Biotropica* 39, 105-113.
- Gascon, C. 1989. Predator-prey size interaction in tropical ponds. *Revista Brasileira de Zoologia* 6, 701-706.
- Gascon C. 1991. Population- and community-level analyses of species occurrences of Central Amazonian rainforest tadpoles. *Ecology* 72, 1731–1746.
- Giarretta A. A. ; Facure K. G. ; Sawaya R. J. ; Meyer J. H. De M.; Chemin N. 1999. Diversity and abundance of litter frogs in a montane forest of Southeastern Brazil: seasonal and altitudinal changes. *Biotropica* 31, 669–674.
- Gordo M.; Carvalho V.T.; Oliveira M.E.; Esteves F.A.D.; Lemos M.; Bernhard R.; Bernardes V.C.D.; Nascente L.B.; Seixas M. 2009. Diagnóstico Ambiental do Parque Nacional do Viruá: Inventário de Herpetologia. Relatório Técnico. ICMBio.
- Gottsberger B. & Gruber E. 2004. Temporal partitioning of reproductive activity in a neotropical anuran community, *Journal of Tropical Ecology* 20, 271–280.
- Halverson M.A; Skelly D.K.; Kiesecker J.M.; Freidenburg L.M. 2003. Forest mediated light regime linked to amphibian distribution and performance. *Oecologia* 134, 360-364.

- Hamilton, S.K.; Sippel, S.J.; Melack, J.M. 2002. Comparison of inundation patterns among major South American floodplains. *Journal of Geophysical Research* 107 (D20), 8038.
- Hero J.M.1990. An illustrated key to tadpoles occurring in the Central Amazon rainforest, Manaus, Amazonas, Brasil. *Amazoniana* 11, 201-262.
- Hero J.M.;Magnusson W. E.; Rocha C. F. D.; Catterall, C. P. 2001. Antipredator defenses influence the distribution of amphibian prey species in the central Amazon rain forest. *Biotropica* 33, 131-141.
- Hero J.M.; Gascon C.; Magnusson,W.E. 1998. Direct and indirect effects of predation on tadpole community structure in the Amazon rainforest. *Australian Journal of Ecology* 23, 474-478.
- Heyer W.R., MCdiarmid R.W. & Weigmann D.L. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica* 7, 100-111.
- Heyer W.R 1969. The adaptative ecology of groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* 23, 421-428.
- Hillers A.; Veith M.; Rödel M-O. 2008. Effects of forest fragmentation and habitat degradation on west african leaf-litter frogs, *Conservation Biology* 22, 762-772.
- Höld W. 1977. Call differences and calling site segregation in anuran species from Central Amazonian floating meadows. *Oecologia* 28,351–363.
- Höld W. 1990. Reproductive diversity in Amazonian lowland frogs. *Fortschritte Zoologie* 38, 41-60.
- Hubbel S.P. 1979.Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203, 1299-1309.
- IBAMA .2008. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. Disponível em: <<http://www.ibama.gov.br/siucweb/mostraUc.php?seqUc=113>>. Acessado em 25 junho 2008.
- Inger, R. F. 1969. Organization of communities of frogs along small rain forest stream in Sarawak. *Journal of Animal Ecology* 38, 123-148.

- Keller A. M.; Rödel E.; Linsenmair E; Grafe T. U. 2009. The importance of environmental heterogeneity for species diversity and assemblages structure in Bornean stream frogs. *Journal of Animal Ecology* 78, 305-314.
- Kenkel N.C. ; Orloci L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* 67, 919–928.
- Kok P.J.R. 2006. A new species of *Hypsiboas* (Amphibia: Anura: Hylidae) from Kaieteur National Park, eastern edge of the Pakaraima Mountains, Guyana. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 76, 191-200.
- Kok P.J.R.; Kalamandeen M. 2008. *Introduction to the taxonomy of the amphibians of Kaieteur National Park, Guyana*. *Abc Taxa*, vol 5, i-ix, 278 p.
- Kruskal J. 1964. Multidimensional scaling by optimizing goodness of fit to nonmetric hypothesis. *Psychometrika* 29, 1–27.
- Laurance W.F.; Fearnside P.M.; Laurance S.G.; Delamonica P.; Lovejoy T.E.; Rankin-de Merona J.; Chambers J.Q. ; Gascon C. 1999. Relationship between soils and Amazon forest biomass: A landscape-scale study. *Forest Ecology and Management* 118, 127-138.
- Lima A. P.; Magnusson W. E.; Menin M.; Erdtmann L. K.; Rodrigues D. J.; Keller C.; Höld W. 2006. *Guia de sapos da Reserva Adolpho Ducke, Amazônia Central*. Atemma, Manaus. 168 p.
- Lips K.; Burrowes P.; Mendelson III J.; Parra-Olea G. 2005. Amphibian population declines in Latin America: a synthesis. *Biotropica* 37, 222- 226.
- Machado R. B.; Aguiar L. M. S.; Ramos-Neto M. B.; Rodrigues F. H. G.; Hass A.; Aquino F. G. 2004. *Atlas de Conservação da natureza brasileira – Unidades Federais*. Metalivros. São Paulo. 335 p.
- Magnusson W. E.; Mourão G. 2005. *Estatística sem matemática*. Editora Planta, Londrina. 138 p.
- Magnusson W. E.; Lima A. P.; Luizão R.; Luizão F.; Costa F. R. C.; Castilho C. V. ; Kinupp V. F. 2005. RAPELD: A modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota neotropica* 5, 1-6.
- Magnusson W.E ; Hero J.M. 1991. Predation and the evolution of complex ovoposition behavior in Amazon rainforest frogs. *Oecologia* 86, 310-318.

- Maltchik L.; Peixoto M.L.; Sturnet C.; Moreira L.F.B.; Machado I.F. (2008) Dynamics of the terrestrial amphibian assemblage in a flooded riparian Forest fragment in a neotropical region in the south of Brazil. *Brazilian Journal Biology* 68, 769-769.
- McCune B.; Grace J.B.; Urban D.L. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.
- McMenamin S.K.; Hadly E.A.; Wright C.K. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proc. Natl. Acad. Sci. USA* 105, 16988-16993.
- Menin M. 2005. *Padrões de distribuição e abundância de anuros em 64km² de floresta de terra-firme na Amazônia Central*. Tese de doutorado, Instituto Nacional de Pesquisas da Amazônia/Universidade Federal do Amazonas, Manaus, Amazonas. 103 pp.
- 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.
- Menin M.; Waldez F.; Lima A. P. 2008. Temporal variation in the abundance and number of species of frogs in 10,000 ha of a Forest in Central Amazonia, Brazil. *South American Journal of Herpetology* 3, 68-81.
- Minchin P.R. 1987. An evaluation of relative robustness of techniques for ecological ordinations. *Vegetatio* 71, 145-156.
- Morand A.; Joly P. 1995. Habitat variability and space utilization by the amphibian communities of the french Upper-Rhone floodplain. *Hydrobiologia* **301**: 249-257.
- Neckel-Oliveira S. 2007. Effects of forest disturbance on breeding habitat availability for two species of anurans in the Amazon. *Copeia* 2007, 186–192.
- Neckel-Oliveira S.; Gascon C. 2006. Abundance, body size and movement patterns of a tropical treefrog in continuous and fragmented forests in the Brazilian Amazon. *Biological conservation* 128, 308-315.
- Oksanen J.; Kindt R.; Legendre P.; O'Hara R.B. 2006. VEGAN: Community Ecology Package. Available from URL: <http://cran.r-project.org>.

- Paton P.W.C.; Crouch, W. B. 2002. Using the phenology of pond breeding amphibians to develop conservation strategies. *Conservation Biology* 16, 194-204.
- Parris K.M.; McCarthy M.A. 1999. What influences the structure of frog assemblages at forest streams? *Australian Journal of Ecology* 24, 495–502.
- Parris K.M. 2004. Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. *Ecograph* 27, 392–400.
- Pazin V.; Magnusson W.E.; Zuanon J.; Mendonça, F. 2006. Fish assemblages in temporary ponds adjacent to “terra firme” streams in Central Amazonia. *Freshwater Biology* 51, 1025-1037.
- Pearman P. B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conservation Biology* 11, 1211–1225.
- Pechmann J. H. K.; Scott D.E; Gibbons J.W.; Semlitsch R.D. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile salamanders. *Wetlands Ecology and Management* 1, 3–11.
- Pounds A. ; Crump M. 1994. Amphibian declines and climate disturbance: the case of the golden toad and the harlequin frog. *Conservation Biology* 8, 72-85.
- 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, Brasil. *Amphibia-Reptilia* 26, 211-221.
- Prado C.P.A. & Haddad C.F.B. 2005. Size-fecundity relationships and reproductive investment in female frogs in the Pantanal, South-Western Brazil. *Herpetological Journal* 15, 181-189.
- Prance G.T. 1980. A terminologia dos tipos de florestas amazônicas sujeitas a inundação. *Acta Amazonica* 10, 495-504.
- R Development Core Team. 2006. R: A Language and Environment for Statistical Computing. Available from URL: <http://cran.r-project.org>.
- Rodriguez D. 2006. *Influência de fatores bióticos e abióticos na distribuição temporal e espacial de girinos de comunidades de poças temporárias em 64 km² de floresta de terra firme na Amazônia central*, Tese de doutorado, Instituto Nacional de Pesquisas da Amazônia/Universidade Federal do Amazonas, Manaus, Amazonas.100 pp.

- Rodriguez L.O. 1992. Structure et organization du peuplement d'anoures de Cocha Cashu, Parc National Manu. Amazonie Péruvienne. *Revue d'Ecologie la Terre et la Vie* 47, 151-197.
- Rojas D. 2010. *Distribuição e abundancia de anuros de florestas de terra firme na fazenda experimental da Universidade Federal do Amazonas- Amazônia central*, Tese de mestrado, Universidade Federal do Amazonas, Manaus, Amazonas. 60 pp.
- Schaefer, C.E.G.R.; Mendonça, B.A.F.; Fernandes-Filho, E. I. 2009. Geoambientes e Paisagens do Parque Nacional do Viruá – RR: Esboço de Integração da Geomorfologia, Climatologia, Solos, Hidrologia e Ecologia. Relatório Técnico. ICMBio.
- Semlitsch R. D. 1985. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum*. *Copeia* 1985, 608–616.
- Semlitsch R. D. ; Bodie J.R. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibian and reptiles. *Conservation Biology* 17, 1219–1228.
- Semlitsch R. D.; Scott D. E.; Pechmann J. H. K.; Gibbons, J. W. 1996. Structure and dynamics of an amphibian community, p. 217-247 In: Cody, M. L.; Smallwood, J.A. (Eds). *Long-term studies of vertebrate communities*. Academic Press, New York.
- Skelly D.K. 1997. Tadpole communities. *American Scientist* 85, 36-45.
- Tocher M.D.; Gascon C.; Meyer J. 2001. Community composition and breeding success of Amazonian frogs in continuous forest and matrix habitat aquatic sites, p. 235-247. In: Bierregaard Jr, R.O; Lovejoy, T.E.; R.C.G Mesquita, R.C.G. (Eds). *Lessons from Amazonia: the ecology and conservation of a fragmented forest* Yale University Press, Connecticut, USA.
- Toledo L.F.; Zina J.; Haddad C.F.B. 2003. Distribuição espacial e temporal de uma comunidade de anfíbios anuros do Município de Rio Claro, São Paulo, Brasil. *Holos Environment* 3, 136–149.
- Toft C.A. 1980. Seasonal variation in populations of Panamanian litter frogs in their prey: a comparison of wetter and drier sites. *Oecologia* 47, 34-38.

- Urban D.; Goslee S.; Pierce K.; Lookingbill, T. 2002. Extending community ecology to landscapes. *Ecoscience* 9, 200-202.
- Valerio-Brun L. 2008. *Riqueza e abundância de anfíbios (Amphibia-Anura), Pantanal de Poconé, Município de Nossa Senhora do Livramento, Mato Grosso, Brasil*. Dissertação de Mestrado, Universidade Federal de Mato Grosso/ Instituto de Biociências, Cuiabá, Matto Grosso. 83 p.
- Van Sluys M.; Vrcibradic D.; Esbérad C.E.L.; Alves M.A.S.; Bergallo H.H.; Rocha C.F.D. 2007. Ecological parameters of the leaf litter frog community of an Atlantic Rainforest area at Ilha Grande, Rio de Janeiro State, Brazil. *Austral Ecology* 32, 254-260.
- Vasconcelos H. L.; Macedo, A. C. C.; Vilhena, J. M. S. 2003. Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. *Studies on Neotropical Fauna and Environment* 38, 115–124.
- Vasconcelos T.S.; Santos T.G.; Rossa-Feres D.C.; Haddad C.F.B. 2009. Influence of the environmental heterogeneity of breeding ponds on anuran assemblages from southeastern Brazil. *Canadian Journal of Zoology* 87, 699-707.
- Veith M.; Lötters S.; Andreone F.; Rödel M.-O. 2004. Measuring and monitoring amphibian diversity in tropical forests. II. Estimating species richness from standardized transect censusing. *Ecotropica* 10, 85-99.
- Von May R.; Donnelly M. A.. 2009 Do trails affect relative abundance estimates of rainforest frogs and lizards? *Austral Ecology* 34: 613 – 620.
- Watling J. I. 2005. Edaphically-biased distributions of amphibians and reptiles in a lowland tropical rainforest. *Studies on Neotropical Fauna and Environment* 40, 15–21.
- Wellborn G. A.; Skelly D. K.; Werner, E. E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology, Evolution, and Systematics* 27, 337-363.
- Woinarski, J.C.Z., Fisher A. & Milne D. 1999. Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern territory, Australia. *Journal of Tropical Ecology* 15: 381-398.

- Wyman R. L. 1988. Soil acidity and moisture and the distribution of amphibians in five forests of Southcentral New York. *Copeia* 1988, 394–399.
- Zimmerman B. L.; Rodrigues M. T. 1990 Frogs, snakes, and lizards or the INPA-WWF reserves near Manaus, Brazil, p. 426-454. In: Gentry, A.H. (Ed). *Four Neotropical Rainforest*. Yale University Press, New Haven.
- 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.; Simberloff D. 1996. An historical interpretation of habitat use by frogs in a central Amazonian forest. *Journal of Biogeography* 23, 27-46.

ANEXO A- ATA AULA QUALIFICAÇÃO



AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): PAULA MERCEDES COCA SOTO
Curso: ECOLOGIA
Nível: MESTRADO
Orientador(a): CLAUDIA KELLER
Co-Orientador(a): ALBERTINA PIMENTEL LIMA

Título:

"Estrutura de comunidade de anuros em uma área de floresta alagável no Parque Nacional do Viruá (Roraima-Brasil)".

BANCA JULGADORA:

TITULARES:

Elizabeth Chilson (INPA)
Celso Morato (INPA)
Flávia Costa (INPA)

SUPLENTES:

Gonçalo Ferraz (INPA)
Renato Cintra (INPA)

EXAMINADORES	PARECER	ASSINATURA
Elizabeth Chilson (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Celso Morato (INPA)	() Aprovado () Reprovado	
Flávia Costa (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Gonçalo Ferraz (INPA)	() Aprovado () Reprovado	
Renato Cintra (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	

Manaus(AM), 20 de março de 2009

OBS: _____

ANEXO B- FICHAS DE AVALIAÇÃO DA BANCA NÃO PRESENCIAL



Instituto Nacional de Pesquisas da Amazônia - INPA



Programa de Pós-graduação em Ecologia

Avaliação de dissertação de mestrado

Título: **Padrões de distribuição de anuros em uma área de 25 Km² em uma floresta sazonalmente alagável no norte da Amazônia brasileira**

Aluno: **PAULA MERCEDES COCA SOTO**

Orientador: **Claudia Keller**

Co-orientador: **Albertina Pimentel Lima**

Avaliador: Cynthia Peralta de Almeida Prado

Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(X)	()	()	()
Revisão bibliográfica	()	(X)	()	()
Desenho amostral/experimental	(X)	()	()	()
Metodologia	(X)	()	()	()
Resultados	()	(X)	()	()
Discussão e conclusões	()	(X)	()	()
Formatação e estilo texto	(X)	()	()	()
Potencial para publicação em periódico(s) indexado(s)	()	(X)	()	()

PARECER FINAL

() **Aprovada**

(X) **Aprovada com correções** (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

() **Necessita revisão** (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

() **Reprovada** (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Jaboticabal, São Paulo

04 de maio de 2010

Local

Data

Assinatura

Avaliação de dissertação de mestrado

Título: **Padrões de distribuição de anuros em uma área de 25 Km² em uma floresta sazonalmente alagável no norte da Amazônia brasileira**

Aluno: **PAULA MERCEDES COCA SOTO**

Orientador: **Claudia Keller**

Co-orientador: **Albertina Pimentel Lima**

Avaliador: Marcelo Menin

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(X)	()	()	()
Revisão bibliográfica	(X)	()	()	()
Desenho amostral/experimental	(X)	()	()	()
Metodologia	(X)	()	()	()
Resultados	(X)	()	()	()
Discussão e conclusões	()	(X)	()	()
Formatação e estilo texto	()	()	(X)	()
Potencial para publicação em periódico(s) indexado(s)	(X)	()	()	()

PARECER FINAL

() **Aprovada**

(X) **Aprovada com correções** (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

() **Necessita revisão** (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

() **Reprovada** (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Manaus-AM,

06 de abril de 2010,



Local

Data

Assinatura

Referee evaluation sheet for MSc thesis

Title: Padrões de distribuição de anuros em uma área de 25 Km² em uma floresta sazonalmente alagável no norte da Amazônia brasileira
 Candidate: PAULA MERCEDES COCA SOTO
 Supervisor: Claudia Keller Co-supervisor: Albertina Pimentel Lima

Examiner: James I. Watling

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	(X)	()	()	()
Literature review	(X)	()	()	()
Sampling design	(X)	()	()	()
Methods/procedures	(X)	()	()	()
Results	(X)	()	()	()
Discussion/conclusions	(X)	()	()	()
Writing style and composition	()	(X)	()	()
Potential for publication in peer reviewed journal(s)	(X)	()	()	()

FINAL EVALUATION

- () Approved without changes
- (X) Approved with changes (no need for re-evaluation by this reviewer)
- () Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)
- () Not acceptable (This product is incompatible with the minimum requirements for this academic level)

Miami, USA

9 May 2010

Place

Date

James I. Watling
Signature

Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and claudiakeller23@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.

Mailing address:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil

ANEXO C- ATA DEFESA PRESENCIAL



ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 30 dias do mês de agosto do ano de 2010, às 14:30 horas, na sala de aula do Programa de Pós-Graduação em Ecologia PPG-ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: Prof(a). Dr(a). **Renato Cintra**, do Instituto Nacional de Pesquisas da Amazônia, Prof(a). Dr(a). **Regina Celi Costa Luizão**, do Instituto Nacional de Pesquisas da Amazônia, Prof(a). Dr(a). **Thierry Ray Jehlen Gasnier**, da Universidade Federal do Amazonas, tendo como suplentes o(a) Prof(a). Dr(a). Richard Carl Vogt, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública da **DISSERTAÇÃO DE MESTRADO** de **PAULA MERCEDES COCA SOTO**, intitulada "Padrões de distribuição de anuros em uma área de 25 Km² em uma floresta sazonalmente alagável no norte da Amazônia brasileira", orientado(a) pelo(a) Prof(a). Dr(a). Claudia Keller, do Instituto Nacional de Pesquisas da Amazônia e co- orientado(a) pelo(a) Dr(a) Albertina Pimentel Lima, do Instituto Nacional de Pesquisas da Amazônia.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

- APROVADO(A) REPROVADO(A)
 POR UNANIMIDADE POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Renato Cintra

Prof(a).Dr(a). Regina Celi Costa Luizão

Prof(a).Dr(a). Thierry Ray Jehlen Gasnier

Flávia Costa
Coordenação PPG-ECO/INPA