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UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
(ZOOLOGIA)

DIVERSIDADE, PADRÕES ESPACIAIS E TEMPORAIS DE ANFÍBIOS ANUROS EM UMA FLORESTA ESTACIONAL SEMIDECIDUAL ATLÂNTICA, PARQUE ESTADUAL DO MORRO DO DIABO (PEMD)

TIAGO DA SILVEIRA VASCONCELOS

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro da Universidade Estadual Paulista “Júlio Mesquita Filho”, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Área de Concentração: Zoologia).

Setembro - 2009

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Orientador: Célio Fernando Baptista Haddad
Co-orientadora: Denise de Cerqueira Rossa-Feres

Setembro - 2009

TIAGO DA SILVEIRA VASCONCELOS

Diversidade, padrões espaciais e temporais de anfíbios anuros em uma Floresta Estacional Semidecidual Atlântica, Parque Estadual do Morro Do Diabo (PEMD)

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro da Universidade Estadual Paulista "Júlio Mesquita Filho", como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Área de Concentração: Zoologia).

COMISSÃO EXAMINADORA

Rio Claro, ___de________________de_______

"Enfim, pode-se dizer que aqui se derruba uma gigantesca perobeira para em seu logar se plantar quatro grãos de milho!! Se a isso se dá o nome de lavoura, eu não sei o que seja destruição!!"

Theodoro F. Sampaio, 1890

"Grandes resultados não podem ser conseguidos de uma vez, e devemos ficar satisfeitos a avançar na vida assim como caminhamos – passo a passo."

Samuel Smiles

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SUMÁRIO

Resumo Geral. A região ocidental do estado de São Paulo abriga a maior área contínua remanescente da Floresta Estacional Semidecidual Atlântica que recobria esta região. Grande parte desta região está protegida no Parque Estadual do Morro do Diabo (PEMD), considerada insuficientemente conhecida, mas de provável importância biológica em relação a herpetofauna. O presente estudo objetivou-se por estudar os padrões de distribuição espacial e temporal da anurofauna do PEMD, e também verificar como a heterogeneidade dos corpos d'água influencia na composição e riqueza de espécies de anfíbios. De maneira geral, as espécies de anfíbios registradas no PEMD (tanto adultos em atividade de vocalização quanto girinos) ocorreram diferentemente entre os variados tipos de corpos d'água amostrados, sendo principalmente relacionado com tipo de correnteza e hidroperíodo dos corpos d'água. Assim, a composição da anurofauna foi diferente entre corpos d'água lóticos, lênticos permanentes/semi-permanentes e lênticos temporários. A ocorrência temporal das espécies foi restrita aos meses quente e úmido do ano (com exceção de uma espécie que ocorreu durante os meses frio e seco), o que resultou em alta sobreposição temporal no período de vocalização dos machos e ocorrência de girinos. Grupos de espécies ocorreram diferentemente ao longo dos meses quente e úmido, com espécies características de início, meio e fim da estação chuvosa. A análise macro-espacial da distribuição da anurofauna no PEMD evidenciou uma baixa similaridade entre as diferentes fitofisionomias amostradas. Na verdade, esta baixa similaridade faunística foi consequência da baixa eficiência de captura das armadilhas de interceptação e queda, o que resultou em uma baixa riqueza de espécies nas fitofisionomias estudadas. No entanto, alta similaridade na composição de espécies foi encontrada somente entre as áreas mais bem preservadas do PEMD, devido à ocorrência de *Rhinella ornata*. Esta espécie foi indicativa da fitofisionomia mais bem preservadas do parque, enquanto duas outras espécies da família Leiuperidae (*Eupemphix nattereri* e *Physalaemus cuvieri*), consideradas generalistas na ocupação de habitat, foram indicadoras da mata em estágio avançado de regeneração. Três dos cinco descritores da heterogeneidade ambiental das poças estudadas influenciaram na composição de espécies de anuros: número de tipos de margem, número de estratificações vegetais presentes nas margens e hidroperíodo das poças. Somente número de tipos de margens foi relacionado com a riqueza de espécie de anuros nas poças estudadas. Porcentagem de cobertura vegetal e tamanho dos corpos d'água não influenciaram na composição e riqueza de espécies nas poças. A correlação de três descritores ambientais das poças com a composição de espécies de anuros e somente um descritor correlacionado com a riqueza de espécie sugere que uma estratégia de conservação efetiva deve primeiramente considerar a composição de espécies, pois corpos d'água com um mesmo número de espécies podem abrigar uma diferente composição de espécies.

Palavras-chave: Domínio da Mata Atlântica, distribuição micro-espacial, distribuição macro-espacial, fenologia reprodutiva, Floresta Estacional Semidecidual, heterogeneidade ambiental.

Abstract. Occidental region of São Paulo state shelters the largest continuous remnant of Mesophytic Semideciduous Forest (Atlantic domain). Most of this region is legally protected by the Morro do Diabo State Park (MDSP), considered insufficient known but with probable biological importance concerning amphibians and reptiles. The present study aimed to study the spatio-temporal patterns of anuran distribution at MDSP, as well as to verify how environmental heterogeneity of breeding ponds influences on richness and anuran species composition. In general, recorded species (either calling males or tadpoles) occurred differentially among the studied breeding habitats, which was mainly related to the water flow and hidroperiod of breeding habitats. Thus, lotic, lentic permanent/semi-permanent, and lentic temporary breeding habitats presented different anuran species composition. Temporal distribution of individuals was restricted to the moist and hot months (with exception to one species that occurred during the dry and cold months), resulting in a high temporal overlap of calling males and tadpoles distribution. Groups of species distributed differentially through the hot and moist months, where typical species of beginning, middle, and end of the rainy season could be identified. A macro-spatial analysis of anuran distribution evidenced low similarity among different sampled phytophysiognomies. Actually, the low faunistic similarity is rather a consequence of the low efficiency of capture by pitfall traps with drift fences, resulting in low species richness in the phytophysiognomies studied. However, a high similarity on species composition was found only among the most preserved areas of MDSP, due to the presence of *Rhinella ornata*. This species was indicative of the most preserved area of the MDSP, while two other species from the Leiuperidae family (*Eupemphix nattereri* and *Physalaemus cuvieri*), which are considered generalists in terms of habitat occupation, were indicative of the forest in advanced regeneration stage. Three out of the five environmental descriptors of the studied breeding ponds influenced on anuran species composition: number of edge types, number of plant types along the edges, and hydroperiod of breeding ponds. Only the number of edge types was related to anuran species richness at the studied ponds. Neither percentage of vegetation cover nor size of breeding ponds influenced on richness and anuran species composition. The correlation of three environmental descriptors with species composition and one environmental descriptor with species richness suggests that an effective conservation strategy must primarily consider the species composition, because breeding ponds with the same number of species can shelter a different species composition.

Key-words: Atlantic forest domain, breeding phenology, environmental heterogeneity, macro-spatial distribution, micro-spatial distribution, Mesophytic Semideciduous Forest.

INTRODUÇÃO

A conservação da diversidade biológica está cada vez mais difícil e complexa, devido principalmente ao crescimento explosivo da população humana, que tem contribuído para a perda de grande parte da diversidade biológica (Wilson, 1997). A diversidade biológica pode ser ameaçada por diversos fatores como destruição e fragmentação de hábitats naturais, degradação e poluição ambiental, superexploração e introdução de espécies exóticas (Primack & Rodrigues, 2002). Contudo, a destruição de hábitats é considerada a principal ameaça à diversidade biológica (Wilson, 1997; Primack & Rodrigues, 2002; Cerqueira *et al.*, 2003). A estimativa de desmatamento de florestas no mundo no final da década de 1980 era de 240.000 km^2 por ano (Bush, 1997), resultando em uma taxa de extinção de 25.000 espécies por ano (Wilson, 1989). Ainda durante a década de 1980, as florestas tropicais do continente americano foram as que sofreram as maiores taxas de desmatamento (Whitmore, 1997). No Brasil, a devastação do bioma Mata Atlântica é um exemplo do intenso processo de ocupação humana, pois atualmente restam menos de 8% de sua extensão original (Mamede *et al.*, 2004), que abrangia aproximadamente 1.000.000 km^2 antes do processo de devastação (Ab'Saber, 2003).

Dentre os diversos grupos animais que sofrem diretamente com as degradações ambientais causadas pelo homem (ver exemplos em Laurance & Bierregaard, 1997), os anfíbios são considerados os mais sensíveis (Stebbins & Cohen, 1997). Isto se deve principalmente a duas características únicas que os anfíbios apresentam: 1) ciclo de vida dependente tanto do ambiente aquático (forma larvária) quanto do ambiente terrestre (forma pós-metamórfica) para a grande maioria das espécies, além da necessidade de um microambiente úmido para o desenvolvimento dos ovos naquelas espécies com ausência da fase larvária; 2) alta permeabilidade da pele, onde é realizada grande parte das trocas gasosas (Duellman & Trueb, 1994; Stebbins & Cohen, 1997). Dentre as principais ameaças à conservação dos anfíbios (*e.g.*, aumento da radiação ultravioleta, chuvas ácidas, doenças infecciosas, introdução de espécies exóticas, resíduos de pesticidas aplicados em culturas agrícolas: Beebee, 1996; Stebbins & Cohen, 1997; Haddad, 1998; Withgott, 2002; Silvano & Segalla, 2005, Doody *et al.*, 2009), a destruição de hábitats naturais é a principal no Brasil e no mundo (Duellman & Trueb, 1994; Silvano & Segalla, 2005).

Apesar do Brasil abrigar a maior riqueza de anfíbios do mundo (849 espécies: SBH, 2009) e de diversos estudos serem publicados ao longo dos anos em diversos campos de pesquisa (*e.g.*, Eterovick & Fernandes, 2001; Aguiar Jr. *et al.*, 2007; Zieri *et al.*, 2007; Giovanelli *et al.*, 2008; Santos *et al.*, 2009), informações básicas sobre história natural, ecologia e mesmo distribuição geográfica para a maioria das espécies brasileiras permanecem desconhecidas (Silvano & Segalla, 2005). Estudos da fase larvária dos anfíbios anuros (girinos) são ainda mais escassos, apesar dos girinos serem um modelo biológico adequado para estudos ecológicos e evolucionários, por formarem comunidades temporais nos corpos d’água onde vivem (Alford, 1999). No Brasil, somente na década de 1970 começaram a surgir na literatura estudos sobre dinâmica de comunidades, aspectos ecológicos da metamorfose e estudos sobre aspectos funcionais e evolutivos da morfologia de girinos (veja breve histórico em Fatorelli & Rocha, 2008).

A dependência da qualidade ambiental tem demonstrado que a estruturação das comunidades de anfíbios anuros é altamente influenciada por fatores abióticos (*e.g.*, chuva, temperatura, heterogeneidade vegetal, tamanho e hidroperíodo dos corpos d’água: Parris, 2004; Bastazini *et al.*, 2007; Afonso & Eterovick, 2007; Keller *et al.*, 2009), sendo que em alguns estudos estes fatores apresentam maior importância na estruturação das comunidades de anfíbios do que fatores bióticos (*e.g.*, predação e competição) (Parris, 2004; Werner *et al.*, 2007). No entanto, a ocorrência espacial de anfíbios anuros em diversos tipos de hábitats (tanto adultos quanto girinos) não pode ser explicada somente por um fator, mas sim por uma interação complexa de fatores bióticos e abióticos (Toft, 1985; Jakob, 2003; Kopp *et al.*, 2006; Fatorelli & Rocha, 2008). Em alguns casos, a distribuição dos táxons entre diferentes ambientes também é explicada pela história filogenética e biogeográfica das espécies (*e.g.*, Williams & Hero, 2001; Fatorelli & Rocha, 2008), ou então por processos estocásticos de nascimento, morte, colonização e extinção das espécies (Tillman, 2004; Chase, 2007). Neste último caso, características próprias das espécies, interação entre as espécies ou heterogeneidade ambiental não influenciariam na distribuição das espécies, havendo assim uma distribuição aleatória entre diferentes hábitats, em conseqüência de processos estocásticos (*e.g.*, Gascon, 1991; Wild, 1996).

Poucos vertebrados terrestres são tão dependentes de um ambiente úmido como os anfíbios, cujo ciclo de vida é fortemente influenciado pela distribuição e abundância de água, geralmente em forma de chuva (McDiarmid, 1994). Desta maneira, a ocorrência temporal da atividade reprodutiva dos anfíbios é fortemente dependente da ocorrência de chuvas, e é resumida em dois padrões básicos: 1) ocorrência contínua ou em quase todos os meses do ano da atividade reprodutiva das espécies que vivem em regiões tropicais não sazonais, ou seja, onde o regime de chuva é contínuo durante o ano; 2) ocorrência da atividade reprodutiva restrita aos meses mais quentes e chuvosos do ano para a maioria das espécies que vivem em regiões temperadas ou tropicais sazonais (Duellman & Trueb, 1994; Vitt & Caldwell, 2009). O regime de chuva contínuo durante o ano em regiões tropicais não sazonais oferece uma maior oportunidade de partilha temporal na ocorrência das espécies de anfíbios (Duellman, 1978). Por outro lado, como resultado da variação de períodos quente/úmido e seco/frio em regiões tropicais sazonais, a ocorrência temporal da maioria das espécies fica sujeita a uma sobreposição temporal durante o período reprodutivo, onde indivíduos de diversas espécies podem estar presentes em um mesmo corpo d'água (*e.g.*, Arzabe, 1999; Prado *et al.*, 2005; Vasconcelos & Rossa-Feres, 2005; Santos *et al.*, 2007).

A correlação entre ocorrência temporal da atividade reprodutiva de anfíbios e regime de chuvas ao longo do ano é usualmente registrada em estudos fenológicos conduzidos na região tropical e sub-tropical brasileira (*e.g.*, Vasconcelos & Rossa-Feres, 2005; Bernarde, 2007; Conte & Rossa-Feres, 2007; Santos *et al.*, 2007). No entanto, alguns outros estudos não encontram tal relação (*e.g.*, Bernarde & Anjos, 1999; Afonso & Eterovick, 2007), ou mesmo registram correlação da ocorrência temporal dos anfíbios somente com outras variáveis climáticas (temperatura: Bertoluci, 1998; Both *et al.*, 2009; Bernarde & Machado, 2001; fotoperíodo: Both *et al.*, 2008). Estes padrões parecem estar associados com o regime de chuvas de cada localidade, já que em regiões onde a chuva é contínua durante o ano, fatores como fotoperíodo e temperatura tendem a ter uma maior influência no controle da atividade reprodutiva dos anfíbios (Duellman & Trueb, 1994; Both *et al.*, 2008).

O bioma Mata Atlântica (*sensu* Ab'Saber, 1977) é apontado como uma das regiões com a maior biodiversidade do mundo, mas extremamente ameaçado pelas ações humanas (Myers *et al.*, 2000). Em relação aos anfíbios anuros, este bioma abriga cerca de 405 espécies que exibem o mais diversificado número de modos reprodutivos em relação a outros biomas brasileiros (Haddad & Prado, 2005). A Floresta Estacional Semidecidual, considerada um sub-domínio da Mata Atlântica, é caracterizada pela perda parcial das folhas como consequência da baixa precipitação pluviométrica durante o inverno (Veloso *et al.*, 1991). Este tipo de floresta é a formação vegetal brasileira que mais sofreu com o processo de desmatamento durante a colonização do país, devido ao solo fértil (propício para a agricultura) e topografia plana, que facilita seu uso para atividades de pastagem para o gado (Faria, 2006). No interior do estado de São Paulo, a Floresta Semidecidual sofreu intenso processo de desmatamento durante o século XX em função da expansão agropecuária, onde inclusive áreas de preservação permanente não foram respeitadas (Faria, 2006). Esta devastação foi mais intensa na região ocidental do estado, sendo que na região do Pontal do Paranapanema (extremo oeste do estado), restam somente 5% de vegetação nativa (São Paulo, 1999). O Parque Estadual do Morro do Diabo (PEMD), localizado nesta região, preserva a maior área contínua remanescente da floresta que recobria a porção ocidental do estado de São Paulo e de estados vizinhos (Durigan & Franco, 2006).

Segundo o Ministério do Meio Ambiente (MMA, 2000), o PEMD é insuficientemente conhecido, mas de provável importância biológica em relação à herpetofauna. Apenas recentemente foi publicada a lista de espécies de anfíbios do PEMD, onde Santos *et al.* (2009) compararam a composição da anurofauna do Parque com outras localidades brasileiras de diferentes biomas. A anurofauna do PEMD (Tabela 1) é basicamente constituída por um misto de espécies típicas dos domínios Atlântico e Cerrado, além de espécies amplamente distribuídas pela América do Sul, geralmente consideradas tolerantes às alterações antrópicas (Santos *et al.*, 2009). No entanto, apesar de estudos de história natural fornecerem a base de conhecimentos necessária e imprescindível para trabalhos de conservação ambiental, preservação de espécies e elaboração de testes e teorias sobre populações e comunidades (Scott & Campbell, 1982; Greene, 1986, 1994), nenhum estudo deste cunho é conhecido para anfíbios na região do PEMD.

Esta é a principal contribuição deste estudo, que está estruturado em quatro capítulos, com diferentes objetivos:

- No primeiro capítulo analisamos como as comunidades de anfíbios anuros (baseada na estimativa de machos em atividade de vocalização) de seis corpos d’água estão espacialmente e temporalmente organizadas. Além disso, com base nos resultados obtidos, foi possível detectar estratégias adequadas para a conservação dos anfíbios do PEMD, que podem ser usadas em futuras reavaliações do atual plano de manejo (Faria, 2006). Este capítulo ainda não foi submetido para publicação, mas está estruturado conforme normas do periódico *Animal Conservation*.
- No segundo capítulo enfocamos a fase larvária dos anfíbios. Testes de modelos nulos e análises de similaridade foram aplicados para verificar como comunidades de girinos de 11 corpos d’água estão espacial e temporalmente estruturadas. Este capítulo também não foi submetido para publicação, mas está estruturado conforme normas do periódico *Acta Oecologica*.
- No terceiro capítulo comparamos a anurofauna de diferentes fitofisionomias do PEMD. A composição de espécies de anfíbios, amostrados por armadilhas de interceptação e queda (*pitfall traps with drift fences*) em cinco diferentes fitofisionomias do PEMD, foi determinada para verificar se existe diferença na composição de espécies entre as áreas amostradas. Também procuramos verificar a presença de espécies indicadoras de cada fitofisionomia. Este capítulo está submetido para publicação no periódico *Amphibia-Reptilia*, e ainda está sob avaliação dos revisores.
- No quarto capítulo analisamos a influência da heterogeneidade ambiental dos corpos d’água (baseado em cinco descritores ambientais) na composição e riqueza de espécies de anfíbios anuros. Além dos corpos d’água localizados no PEMD, foram incluídos outros 28 corpos d’água localizados na região noroeste do estado de São Paulo, cuja vegetação original era constituída por Floresta Estacional Semidecidual, com clima e composição da

anurofauna bastante similar à da região do PEMD. Este procedimento foi adotado pois a adição de mais corpos d'água tende a minimizar o erro tipo I em análises estatísticas (rejeitar uma hipótese nula quando ela é de fato verdadeira; *sensu* Zar, 1999). Este capítulo está publicado no periódico *Canadian Journal of Zoology* (2009, volume 87, número 8: 699-707).

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Tabela I. Lista de anfíbios anuros do Parque Estadual Morro do Diabo (PEMD), SP (Santos *et al.*, 2009).

FAMÍLIA		ESPÉCIES
Bufonidae	**02 espécies**	*Rhinella ornata* (Spix, 1824)
		Rhinella schneideri (Werner, 1894)
Cycloramphidae	**01 espécie**	*Odontophrynus americanus* (Duméril & Bibron, 1841)
Hylidae	**14 espécies**	*Dendropsophus minutus* (Peters, 1872)
		Dendropsophus nanus (Boulenger, 1889)
		Hypsiboas albopunctatus (Spix, 1824)
		Hypsiboas faber (Wied-Neuwied, 1821)
		Hypsiboas lundii (Burmeister, 1856)
		Hypsiboas punctatus (Schneider, 1799)
		Hypsiboas raniceps Cope, 1862
		Itapotihyla langsdoffii (Duméril & Bibron, 1841)
		Pseudis platensis Gallardo, 1961
		Scinax berthae (Barrio, 1962)
		Scinax fuscomarginatus (Lutz, 1925)
		Scinax fuscovarius (Lutz, 1925)
		Scinax similis (Cochran, 1952)
		Trachycephalus venulosus (Laurenti, 1768)
Leiuperidae	**02 espécies**	*Eupemphix nattereri* Steindachner, 1863
		Physalaemus cuvieri Fitzinger, 1826
Leptodactylidae	**07 espécies**	*Leptodactylus chaquensis* Cei, 1950
		Leptodactylus fuscus (Schneideri, 1799)
		Leptodactylus labyrinthicus (Spix, 1824)
		Leptodactylus mystaceus (Spix, 1824)
		Leptodactylus mystacinus (Burmeister, 1861)
		Leptodactylus cf. *ocellatus* (Linnaeus, 1758)
		Leptodactylus podicipinus (Cope, 1862)
Microhylidae	**02 espécies**	*Chiasmocleis albopunctata* (Boettger, 1885)
		Elachistocleis bicolor (Guérin-Méneville, 1838)

Photo: T. G. dos Santos

CAPÍTULO 1

SPATIO-TEMPORAL DISTRIBUTION OF ANURANS IN SOUTHEASTERN BRAZIL: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT IN A SEASONALLY DRY TROPICAL FOREST

Spatio-temporal distribution of anurans in southeastern Brazil: implications for conservation and management in a seasonally dry tropical forest

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Abstract. Morro do Diabo State Park (MDSP) represents one of the four largest remnants of Semideciduous Mesophytic Forest (Atlantic Forest domain) in Brazil, but no ecological studies on amphibians are available for this area. In the present study, we aimed to 1) determine how the anuran assemblages are spatially and temporally structured in the MDSP; 2) test for indicator species at different types of the breeding ponds studied; 3) determine conservation implications for future conservation strategies. Similarity analyses revealed a high variation in species composition among the six breeding habitats studied, whereas ponds with similar hydroperiods shared similar anuran species composition, which can be related to interspecific differences in life history traits among species (*e.g.*, length of the larval developmental period). Indicator Species Analysis showed one species as indicator of the studied stream (*Rhinella ornata*), one species as indicator of permanent ponds (*Scinax fuscovarius*), two species as indicators of temporary ponds (*Chiasmocleis albopunctata* and *Elachistocleis bicolor*), and three species as indicators of the semi-permanent pond (*Hypsiboas raniceps*, *Leptodactylus fuscus*, and *Trachycephalus venulosus*). Temporal distribution of species was restricted to the rainy/warmest months (except for *Rhinella ornata*), in agreement with the pattern recorded for seasonal tropical areas. The limited presence during the rainy/warmest months resulted in temporal overlap within guilds of species. Thus, the partitioning of species among breeding habitats and the temporal overlap among species allow us to conclude that space is more important than temporal dimension for permitting species coexistence at MDSP. Some conservation implications that resulted from the present study are: the inclusion of different types of breeding habitats (considering streams and ponds with different hydroperiods) for future conservation strategies, which will protect the species with different reproductive patterns;

and the management of breeding ponds, including the removal of the non-native fish species, *Tilapia rendalli* (Cichlidae) that feed on tadpoles.

Keywords. Atlantic Forest domain, calling males, conservation implications, Semideciduous Forest, phenology, similarity analysis, spatial partitioning, temporal overlap.

Introduction

The conservation of biological diversity has been mainly negatively affected by the explosive growth of human population, which contributes to the loss of biodiversity by means of habitat destruction (Wilson, 1997). At the end of the 1980s, estimation of worldwide deforestation was 240,000 km^2/year (Bush, 1997), which in turn resulted in an extinction rate of 25,000 species/year (Wilson, 1989). In Brazil, the Atlantic Forest biome, which originally accounted for 1,000,000 km^2 (Ab'Saber, 2003), is an example of the intense process of human occupation on the eastern Brazilian coast, which resulted in fragmented landscapes of less than 8% of their original extensions (Mamede *et al.*, 2004). Thus, Atlantic Forest is considered one of the richest but most endangered ecoregions of the world (Myers *et al.*, 2000).

Amphibians in particular are highly dependent on habitat quality, because their life cycle is generally comprised of an aquatic larvae and a terrestrial post-metamorphic phase for the large majority of species, and those species with direct development depend on the moist environment for the development of eggs (Duellman & Trueb, 1994). In addition, most gas exchange occurs through their skin, which also needs moist environments to maintain humidity and, consequently, efficient gas exchange (Duellman & Trueb, 1994).

Thus, the extinction of species or new presence of generalist species in degraded areas makes amphibians good bioindicators of habitat quality (Beebee, 1996; Krishnamurthy, 2003). Major threats to amphibians are habitat loss, climate change, chytridiomycosis, and invasive species, among other (e.g., Eterovick *et al.*, 2005; Silvano & Segalla, 2005; Doody *et al.*, 2009). In Brazil habitat loss is considered the main threat to this animal group (Silvano & Segalla, 2005). Immediate consequences of habitat loss are population removal, isolation in the remnant fragment, and loss of genetic variability (Silvano *et al.*, 2003). In the long term, the isolated populations will be subjected to inbreeding and genetic drift, which in turn reduces their capacities for adaptation, and finally become extinct (Primack & Rodrigues, 2002; Liao & Reed, 2009).

In Brazil, the Mesophytic Semideciduous Forest is considered a sub-domain of the Atlantic Forest domain (*sensu* Ab'Saber, 1977), characterized by the partial loss of leaves during the winter as a consequence of low rainfall during this period (Veloso *et al.*, 1991). This kind of forest experienced the most large-scale deforestation among Brazilian vegetation formations, due to its fertility soil (propitious for agricultural use) and flat topography, which facilitates the use of soil for cattle breeding (Faria 2006a). In the westernmost region of São Paulo state (southeastern Brazil), the Mesophytic Semideciduous Forest was reduced to approximately 5% of its original distribution, and the Morro do Diabo State Park (MDSP) comprises one of the four largest protected areas with this kind of vegetation in Brazil, and is considered to have high biological importance (Faria, 2006a). However, ecological studies regarding amphibians from MDSP are not available. The only study with amphibians in this area was documented recently, in which Santos *et al.* (2009) published a species list of the area and discussed its species composition with other Brazilian localities. In the present study, we hypothesized that anurans at MDSP are spatially and temporally structured, since different anuran species have been documented to respond differentially to various environmental characteristics of breeding ponds (e.g., Parris & McCarthy, 1999; Keller *et al.*, 2009; Vasconcelos *et al.*, 2009), and are highly dependent on climatic variation during the year (e.g., Duellman & Trueb, 1994; Vasconcelos & Rossa-Feres, 2005; Kopp & Eterovick, 2006). Thus, we aimed to 1) determine how the anuran assemblages are spatially and temporally structured in the MDSP; 2) test for indicator species at different types of studied breeding ponds; and 3) determine the implications for future conservation strategies.

Material and methods

Study site

Morro do Diabo State Park (MDSP), located in the Pontal do Paranapanema region (the westernmost region of São Paulo State, southeastern Brazil), is in a transition area between Cerrado and Atlantic Forest domain (Ab'Saber, 2003). The total area of MDSP accounts for 33,845 ha (Durigan & Franco, 2006), and its phytophysiomic predominance is composed of the Mesophytic Semideciduous Forest and a small patch of Cerrado *sensu stricto*, i.e. savanna-like vegetation in the northern region of the reserve (Durigan & Franco, 2006). Climate in this region is characterized as subtropical with dry winters and wet summers, and historical records indicate a mean of temperature of 22 °C and annual rainfall ranging from 1,100 to 1,300 mm (Faria, 2006b). Additional information on MDSP characterization and map of the studied site is available from Faria (2006a), Santos *et al.* (2009), and Vasconcelos *et al.* (2009).

Sampling procedures

In this study we selected six breeding habitats with different physiognomic and structural characteristics, in order to represent the different types of water bodies available for breeding activities of anurans at MDSP: one stream, one permanent pond, one permanent swamp, one semi-permanent pond, and two temporary ponds (Table 1). Although both permanent and semi-permanent categories are used for breeding ponds that did not dry up throughout the studied period, we considered the semi-permanent pond that one which had its water volume reduced by at least 90% of their maximum volume. Thus, the semi-permanent pond can be classified as an intermediate between permanent and temporary ones, because they do not dry up completely throughout the season, but may have their predator fish abundance strongly reduced at its lowest water volume (T. S. Vasconcelos and T. G. Santos, unpublished report).

From February 2006 to March 2007, each breeding habitat was monthly monitored by survey at breeding sites (*sensu* Scott & Woodward, 1994). The surveys consisted of an abundance estimation of calling males for each species present, with a slow walk through the edge and/or inside the breeding habitats, during the nocturnal period (from sunset, when most species started the calling activities, to the midnight, when most species reduced their calling activities, T.S. Vasconcelos and T.G. Santos, unpublished data). Thus, the time spent in each breeding habitat varied according to its structural complexity and number of anuran species participating in calling activities (Scott & Woodward, 1994). Voucher specimens were deposited in the DZSJRP (UNESP/São José do Rio Preto, São Paulo state, Brazil) and CFBH (UNESP/Rio Claro, São Paulo state, Brazil) anuran collections.

Statistical Analyses

Analysis of breeding habitat occupancy of calling males was performed qualitatively and quantitatively: the presence/absence of calling males in each breeding habitat was analyzed using the Jaccard coefficient (C_J: Magurran, 1988), and beta diversity (i.e. the variation in species composition among sites) between pairs of compared breeding habitats was considered high when $C_J \leq 0.50$; the abundance of each species was considered under the Morisita-Horn index of similarity (Krebs, 1999). The total abundance of each species in each breeding habitat was measured based on the month with the highest abundance record, in order to avoid the overestimation resulted from the sum of sequential samples (for a detailed discussion, see Bertoluci & Rodrigues, 2002; Gottsberger & Gruber, 2004; Vasconcelos & Rossa-Feres, 2005).

The Indicator Species Analysis (ISA) (Dufrêne & Legendre, 1997) was performed in order to test the presence of indicator species of the different kinds of breeding habitats studied at MDSP (lotic, lentic permanent, lentic semi-permanent, and lentic temporary breeding habitats). This method of analysis combines information on the concentration of species abundance in a particular group (i.e. in a particular type of breeding habitat) and the faithfulness of the presence of a species in a particular breeding habitat, and here we consider monthly species abundance in each habitat. It produces Indicator Values (IV) for each species in each group, varying from 0 (no indication) to 100 (perfect indication) (McCune & Mefford, 1999). Statistical significance of IV was tested using the Monte Carlo permutation test (10,000 replicates). ISA was performed using PC-ORD software for Windows (McCune & Mefford, 1999).

Temporal occurrence of species was measured monthly for the abundance of species in all breeding habitats studied, and species were then compared using the Morisita-Horn index of similarity (Krebs, 1999). For spatial and temporal similarity analyses, we $\log_{(X+1)}$ transformed the total abundance of each species, in order to downweight the contributions of quantitatively dominant species. A subsequent cluster analysis (unweighted mean method, UPGMA) was applied in the resultant matrix and clusters were considered when similarity was ≥ 50%. A Cophenetic Correlation Coefficient (r) was calculated in order to verify how much the resulting graph of cluster analysis represents the original similarity matrix, where $r > 0.9$ represents a very good fit, 0.9 – 0.81 represents a good fit, 0.8 – 0.7 represents a poor fit, and $r < 0.7$ represents a very poor fit (Rohlf, 2000). Similarity analyses and Cophenetic Correlation Coefficient were performed using NTSYSpc2.10 software (Rohlf 2000).

Results

We recorded 21 anuran species participating in calling activity, belonging to five different families in the six breeding habitats monitored at MDSP (Table 2). Species richness at each breeding habitat varied from five (in the Stream) to 12 (in the Permanent Swamp and Semi-Permanent Pond) (Table 2). Beta diversity was considered high between pairs of breeding habitats monitored, whereas only the Temporary Pond 1 and 2 pair showed low beta diversity (Table 3).

Similarity analysis of breeding habitats (Figure 1), using the abundance of calling males, revealed two clusters composed of: 1) permanent and semi-permanent breeding habitats, which were mainly characterized by sharing species with prolonged reproductive patterns (*sensu* Wells, 1977) - *Dendropsophus minutus* and *Hypsiboas faber*; and 2) temporary breeding habitats, mainly characterized by sharing species with explosive reproductive patterns (*sensu* Wells, 1977) - *Chiasmocleis albopunctata* and *Scinax berthae*. The analysis set the Stream apart from the other breeding habitats (Figure 1). Indicator

Species Analysis showed that *Rhinella ornata* was characteristic of the lotic breeding habitat (Stream), that *Scinax fuscovarius* was characteristic of permanent lentic breeding habitats (Permanent Pond and Swamp), *Hypsiboas raniceps*, *Trachycephalus venulosus*, and *Leptodactylus fuscus* were characteristics of semi-permanent lentic breeding habitats (Semi-Permanent Pond), and *S. berthae* and *Chiasmocleis albopunctata* were characteristics of temporary lentic breeding habitats (Temporary Ponds 1 and 2) (Table 4).

Temporal occurrence of most species was restricted to the rainy/warm season (Figure 2). During the dry/cold months (from April to August), when monthly rainfall was lower than 50 mm (except for July, when rainfall reached 70 mm), only males of *Rhinella ornata* called in the MDSP stream studied (Figure 2). Although temporal overlap occurred for most species during the rainy season months, similarity analysis (Figure 3) showed partitioning among three groups of species: 1) species that exhibited prolonged reproductive patterns, occurring throughout the rainy season and/or in those months in which rainfall was most abundant (*Dendropsophus minutus*, *D. nanus*, *Hypsiboas faber*, *Hypsiboas raniceps*, *Leptodactylus podicipinus*, *Physalaemus cuvieri*, *Scinax fuscomarginatus*, and *S. fuscovarius*); 2) species in higher abundance or that were found exclusively at the end of the rainy season of 2006 (*Elachistocleis bicolor* and *Scinax berthae*); 3) species that exhibited explosive reproductive patterns after heavy rains in December 2006 (*Chiasmocleis albopunctata*, *Pseudis platensis,* and *Scinax similis*), and species that also occurred after sporadic or heavy rains at the beginning of the rainy season (between August and December 2006: *L. fuscus*, *L. mystaceus*, *L. mystacinus*, and *Trachycephalus venulosus*).

Discussion

Animals have long been recognized to partition environmental resources in three basic ways: temporally, spatially, and trophically (Pianka, 2000). Such differences in each resource dimension reduce competition, and will ultimately allow for the coexistence of a variety of species (Pianka, 1973). According to Toft (1985), space is the first resource axis most partitioned by frogs, and various studies have recorded habitat partitioning among anuran assemblages from different regions of the world, in both descriptive studies (e.g., Bernarde & Machado, 2001; Bertoluci & Rodrigues, 2002; Duellman, 2005) and studies with a statistical approach (e.g., Peltzer *et al.*, 2006; Santos *et al.*, 2007; Vignoli *et al.*, 2007; Keller *et al.*, 2009; Vasconcelos *et al.*, 2009). Explanations for an active choice of breeding habitats by adult anurans are generally related to the physiological adaptations and ecological preferences of species (e.g., Heyer *et al.*, 1975; Bosh & Martínez-Solano, 2003), the effects of environmental variables (e.g., Burne & Griffin, 2005; Keller *et al.*, 2009), and even phylogenetic constraints (Zimmerman & Simberloff, 1996). In the current study, habitat partitioning was exemplified through the high beta diversity among the breeding habitats studied, and also through the segregation of breeding habitats with different water flow and hydroperiods.

In the lotic breeding habitat studied here, only five species were recorded in calling activity. Low anuran species richness in lotic habitats have been frequently recorded in different regions of Brazil (e.g., Gascon, 1991; Bernarde & Machado, 2001; Brasileiro *et al.*, 2005; Vasconcelos & Rossa-Feres, 2005), and, for most species, is largely associated with the lack of reophilic adaptations in the tadpole phase, and the high tadpole predation pressure from fish (Gascon, 1991). Species abundance was also relatively low in the stream studied at MDSP, except for *Rhinella ornata*, whose aggregations of calling males were recorded during the dry season months (July and August 2006). In fact, Indicator Species Analysis revealed *R. ornata* to be characteristic of the lotic breeding habitat of MDSP. In the MDSP, streams are located inside the well preserved areas of the park, and the association of the *R. ornata* with well preserved areas is an important finding for conservation purposes, because *R. ornata* is generally associated with forested areas throughout its geographical distribution (e.g., Baldissera *et al.*, 2004; Brasileiro *et al.*, 2005; Bertoluci *et al.*, 2007). Its absence in areas where native Mesophytic Semideciduous Forest was converted to agricultural activities, in northwestern São Paulo state, may be correlated with the habitat destruction (for complete discussion see Santos *et al.*, 2009).

In this study species composition was different between temporary ponds and permanent/semi-permanent ponds. We believe that a wide number of factors may be interacting in the structure of the anuran assemblages of MDSP (e.g., the number of plant stratifications and the edge types of the ponds: Vasconcelos *et al.*, 2009; the size of the ponds: Afonso & Eterovick, 2007; Keller *et al.*, 2009), but one pattern that is clearly observed in the present study is the relationship between the hydroperiod of the ponds (shown by the different clusters in similarity analysis) and the reproductive patterns exhibited by the species (*sensu* Wells, 1977). In fact, Vasconcelos *et al.* (2009) analyzed the influence of habitat heterogeneity of breeding ponds of the MDSP and other ponds located in the northwestern São Paulo state, and found a pattern of species turnover across the hydroperiod gradient. Wells (1977) identified two basic patterns of reproduction in anurans: prolonged and explosive breeding. These two patterns represent the two ends of a continuum from single-night breeding in some species to year-round breeding in others. As recorded by Both *et al.* (2009), species with similar life history traits tended to be found in breeding habitats with similar hydroperiod. Thus, the permanent and semi-permanent ponds shared species, more related to the prolonged breeding pattern, such as *Dendropsophus minutus* and *Trachycephalus venulosus*, whose calling males were active for a minimum of three months, *Leptodactylus fuscus*, which was recorded for five consecutive months, and *Hypsiboas faber* whose males called in almost all months of the rainy season. On the other hand, temporary breeding ponds shared species related to the explosive breeding pattern, such as *Chiasmocleis albopunctata*, *Elachistocleis bicolor*, and *Scinax berthae,* which occurred opportunistically after heavy rains in temporary ponds. The importance of the hydroperiod of the ponds for anurans seems to be related to the interspecific differences in life history traits of the species (e.g., the length of the larval developmental period and different skills for avoiding strong predator pressure; Babbitt & Tanner, 2000), because tadpoles in temporary ponds should have adaptations for permitting a rapid development before the pond dries, and tadpoles in permanent ponds should minimize predation pressure by means of behavioral and/or physiological adaptations (Woodward, 1983; Kats *et al.*, 1988). For instance, time of tadpole development of *Elachistocleis bicolor* in one of the temporary ponds studied was approximately one month long, whereas time of tadpole development of *Hypsiboas faber* in a permanent pond can be a minimum of five months long (T.S. Vasconcelos and T.G. Santos, unpublished data).

Indicator Species Analysis has shown that *Scinax fuscovarius* is associated with permanent breeding ponds at MDSP. Although this species occurs preferentially in permanent ponds (e.g., Jim, 1980; Both *et al.*, 2008; present study), its presence in temporary ponds is well documented in other areas, which characterize this species as generalist in terms of habitat occupation (Jim, 1980; Achaval & Olmos, 2003; Eterovick & Sazima, 2004; Brasileiro *et al.*, 2005; Vasconcelos & Rossa-Feres, 2005). In MDSP, calling males and tadpoles of *S. fuscovarius* were found during the most of the rainy season months (T.S. Vasconcelos & T.G. Santos, unpublished data), and can therefore be classified as prolonged breeder.

Temporary breeding habitats were indicated by two species: *Chiasmocleis albopunctata* and *Scinax berthae*. This association emphasizes the relationship between species trait and hydroperiod of ponds, since these species were typical explosive breeders that occurred only in temporary ponds at MDSP. These species are also typical of temporary ponds in other areas (Achaval & Olmos, 2003; Toledo *et al.*, 2003; Aquino *et al.*, 2004; Lavilla *et al.*, 2004; Brasileiro *et al.*, 2005; Silva *et al.*, 2009), but the presence in permanent ponds has also been recorded for *S. berthae* (e.g., Vasconcelos & Rossa-Feres, 2005; Conte & Rossa-Feres, 2007; Santos *et al.*, 2008). Reproductive patterns of these species can also be characterized as explosive in other areas (e.g., Toledo *et al.*, 2003; Conte & Rossa-Feres, 2007).

Three species were indicative of the semi-permanent breeding pond: *Hypsiboas raniceps*, *Leptodactylus fuscus*, and *Trachycephalus venulosus*. These species have a wide range of distribution throughout South America (*T. venulosus* can also be found in Central America: IUCN, 2008; Frost *et al.*, 2009), and live in both well preserved and degraded/urban habitats (La Marca *et al.*, 2004a, b; Reynolds *et al.*, 2004). Thus, the adaptations that make it possible for them to survive in degraded areas should also have favored them to occupy the semi-permanent pond studied, which have restrictive characteristics for several amphibian species, typical of both temporary ponds (a severe reduction in water volume during the dry season - up to 90% of its total volume) and permanent ponds (presence of fish that feed on tadpoles: *Astyanax altiparanae* – Characidae, and the non-native *Tilapia rendalli* – Cichlidae, unpublished report).

Because rainfall and temperature are the major determinants for the timing of breeding activities (Duelman & Trueb, 1994; Vitt & Caldwell, 2009), the temporal occurrence of great majority of calling males was restricted to the months with the highest rainfall and temperature values. There are two general patterns that can be recognized regarding breeding activities of amphibians: year-round or extended breeding activity in amphibian communities living in aseasonal tropical environments, i.e. in places where there is no distinguishable dry or wet season, but rather, continuous rainfall throughout the year; and seasonal breeding activity that generally occurs in the warmest and moist months of the year in temperate and seasonal tropical regions (Duellman & Trueb, 1994; Vitt & Caldwell, 2009). Seasonal breeding and calling activities have long been recorded in tropical and subtropical regions of Brazil (e.g., Prado *et al.*, 2005; Bernarde, 2007; Canelas & Bertoluci, 2007; Both *et al.*, 2008), but studies that effectively assess how much species partition temporal dimension are scarce (Vasconcelos & Rossa-Feres, 2005; Santos *et al.*, 2007; Both *et al.*, 2008; Santos *et al.*, 2008). Among these studies, the partitioning of temporal occurrence can be seen among three or four clusters of species, but there is a relatively high number of species overlapping within clusters (Vasconcelos & Rossa-Feres, 2005; Santos *et al.*, 2007, 2008; Both *et al.*, 2008). In the present study, overlap was recorded among eight species that occurred throughout the rainy season and/or in those months during which rainfall/temperature was higher (cluster 1 in Figure 3), which agrees with the pattern recorded by Vasconcelos & Rossa-Feres (2005), Santos *et al*. (2007 and 2008), and Both *et al.* (2008). Toft (1985) concluded that time is the second resource axis most partitioned by adult amphibians (space is the first one). The findings of our study (the partitioning of species among breeding habitats, and temporal occurrence of most species being restricted to the rainy/warmest season, resulting in overlap) allow us to conclude that space is more important than temporal dimension for permitting species coexistence at MDSP.

Conservation Implications

Since the MDSP represents one of the four largest remnants of Mesophytic Semideciduous Forest in Brazil (Faria, 2006a), the present study provides important findings that support future conservation strategies and management at the site studied, as well as in other sites with Mesophytic Semideciduous Forest vegetation.

Because of the species turnover across the different breeding habitats at MDSP (high beta diversity), an effective conservation strategy would be the protection of large areas, which would assure the inclusion of the different types of breeding habitats found at MDSP. This strategy has been previously proposed by Babbitt (2005), who suggested the inclusion of ponds with different hydrological gradients for more efficient amphibian protection. The protection of ponds with different hydrological gradients will safeguard the species with different reproductive patterns in the area studied. In addition, the inclusion of streams in the most preserved areas inside the MDSP will also contribute to the protection of *Rhinella ornata*, a toad species that was possibly affected in other areas where its natural habitat was converted to agricultural landscape, and *Hypsiboas lundii*, not recorded herein, but which is also found only in a well preserved stream inside the MDSP) (Santos *et al.*, 2009).

Since the aggregations of amphibians at individual breeding ponds may not represent distinct populations, we do not recommend the management of breeding ponds as distinct units (Marsh & Trenham, 2001), but rather, using the metapopulation dynamic. In this way, we suggest the protection of areas surrounding the breeding ponds, because during the migration process of adult anurans between forest remnants and breeding ponds, habitat disconnection adversely affects anuran richness in local assemblages that depend on aquatic environments for reproduction (Becker *et al.*, 2007).

Because deterministic processes frequently drive amphibian populations to extinction, simply protecting clusters of breeding ponds may not be sufficient for maintaining viable populations. Instead, active management may be necessary to protect amphibian populations (Marsh & Trenham, 2001), as well as the removal of non-native predators (especially in the semi-permanent pond where the non-native fish *Tilapia rendalli*, which feeds on tadpoles, is found). The construction, maintenance, and monitoring of breeding ponds, using the environmental descriptors pointed out by Vasconcelos *et al.* (2009) as important predictors for species compositions in the area studied, are also recommended. Finally, we suggest the consideration of climatic variables (particularly rainfall) for the management of temporary ponds (Paton & Crouch, 2002), such as the construction of temporary ponds before heavy rains of a given year, because time of the year and quantity of rainfall affects the calling activity of anurans, as well as the duration of temporary ponds.

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Table 1. Main characteristics of the six studied anuran breeding habitats in MDSP, São Paulo state, southeastern Brazil. PP = Permanent Pond, PS = Permanent Swamp, S = Stream, SPP = Semi-Permanent Pond, TP = Temporary Pond.

	Geographic co-ordinates	**Total area**	**Hydroperiod**	**Surrounding environment**
PP	22°22’10.2’’S; 52°19’43.0’’W	2000m^2	Permanent	Forest edge
PS	22°37’01.0’’S; 52°10’08.8’’W	900m^2	Permanent	Open area
S	22°36’16.3’’S; 52°18’04.2’’W	2655m^2	Permanent	Forest
SPP	22º32’43,7’’S; 52º14’02,9’’W	900m^2	Semi-permanent	Forest edge
TP1	22º37’02,2’’S; 52º10’01,4’’W	300m^2	Temporary	Forest
TP2	22º37’06,8’’S; 52º10’05,9’’W	100m^2	Temporary	Open area

Table 2. Anurans recorded in the six monitored breeding habitats at MDSP, São Paulo state, southeastern Brazil, from February 2006 to March 2007. S = Stream, PP = Permanent Pond, PS = Permanent Swamp, SPP = Semi-Permanent Pond, TP = Temporary Pond.

	S	**PP**	**PS**	**SPP**	**TP1**	**TP2**
Bufonidae						
Rhinella ornata	12	0	0	0	0	0
Hylidae						
Dendropsophus minutus	0	0	30	11	0	0
D. nanus	0	5	90	35	1	20
Hypsiboas albopunctatus	1	1	0	0	0	0
H. faber	0	19	0	8	0	0
H. raniceps	0	4	1	10	4	1
Pseudis platensis	0	0	1	0	0	0
Scinax berthae	0	0	0	0	16	5
S. fuscomarginatus	0	0	35	0	0	0
S. fuscovarius	0	19	10	0	0	13
S. similis	0	0	70	0	0	0
Trachycephalus venulosus	1	0	3	6	0	0
Leiuperidae						
Eupemphix nattereri	0	6	0	0	0	0
Physalaemus cuvieri	0	66	15	43	3	10
Leptodactylidae						
Leptodactylus fuscus	0	4	1	32	0	0
L. mystaceus	2	0	0	1	7	1
L. mystacinus	0	9	0	3	3	2
L. cf. *ocellatus*	0	0	0	1	0	0
L. podicipinus	1	13	3	7	25	20
Microhylidae						
Chiasmocleis albopunctata	0	0	0	0	7	13
Elachistocleis bicolor	0	0	1	4	15	7
Total Richness	5	10	12	12	9	10

Table 3. Similarity among the six monitored breeding habitats at MDSP, São Paulo state, southeastern Brazil, considering presence/absence of calling males at each breeding habitat (Jaccard coefficient). High beta diversity between combinations pairs are highlighted in Bolt ($C_J \leq 50\%$). Numbers in Italics means the number of shared species between breeding habitats. S = Stream, PP = Permanent Pond, PS = Permanent Swamp, SPP = Semi-Permanent Pond, TP = Temporary Pond.

	S	PS	PP	SPP	TP1	TP2
S	*	**13.33**	**15.38**	**21.43**	**16.67**	**15.38**
PS	*2*	*	**37.5**	**50**	**31.25**	**37.5**
PP	*2*	*6*	*	**46.67**	**35.71**	**42.86**
SPP	*3*	*8*	*7*	*	**50**	**46.67**
TP1	*2*	*5*	*5*	*7*	*	90
TP2	*2*	*6*	*6*	*7*	*9*	*

Table 4: Species Indicator Analysis (ISA) for spatial distribution of anuran species in the four types of studied breeding habitats, from February 2006 to March 2007, at the MDSP, São Paulo state, southeastern Brazil. Groups: 1) Lotic breeding habitat, 2) Permanent breeding habitats, 3) Semi-Permanent breeding habitat, 4) Temporary breeding habitats. Indicator values (IV) and statistical significance (p); ns = p>0.05.

Species	Group	IV	p
Rhinella ornata	1	14.3	0.047
Dendropsophus minutus	3	9.6	0.108
D. nanus	2	14.3	0.255
Hypsiboas albopunctatus	1	3.6	0.882
H. faber	3	15.8	0.065
H. raniceps	3	20.0	0.045
Pseudis platensis	2	3.6	1.000
Scinax berthae	4	14.3	0.046
S. fuscomarginatus	2	10.7	0.170
S. fuscovarius	2	20.5	0.016
S. similis	2	7.1	0.261
Trachycephalus venulosus	3	15.1	0.036
Eupemphix nattereri	2	3.6	1.000
Physalaemus cuvieri	3	17.7	0.116
Leptodactylus fuscus	3	20.8	0.022
L. mystaceus	1	5.4	0.651
L. mystacinus	2	10.1	0.458
L. cf. *ocellatus*	3	7.1	0.322
L. podicipinus	4	11.9	0.482
Chiasmocleis albopunctata	4	14.3	0.041
Elachistocleis bicolor	4	14.0	0.095

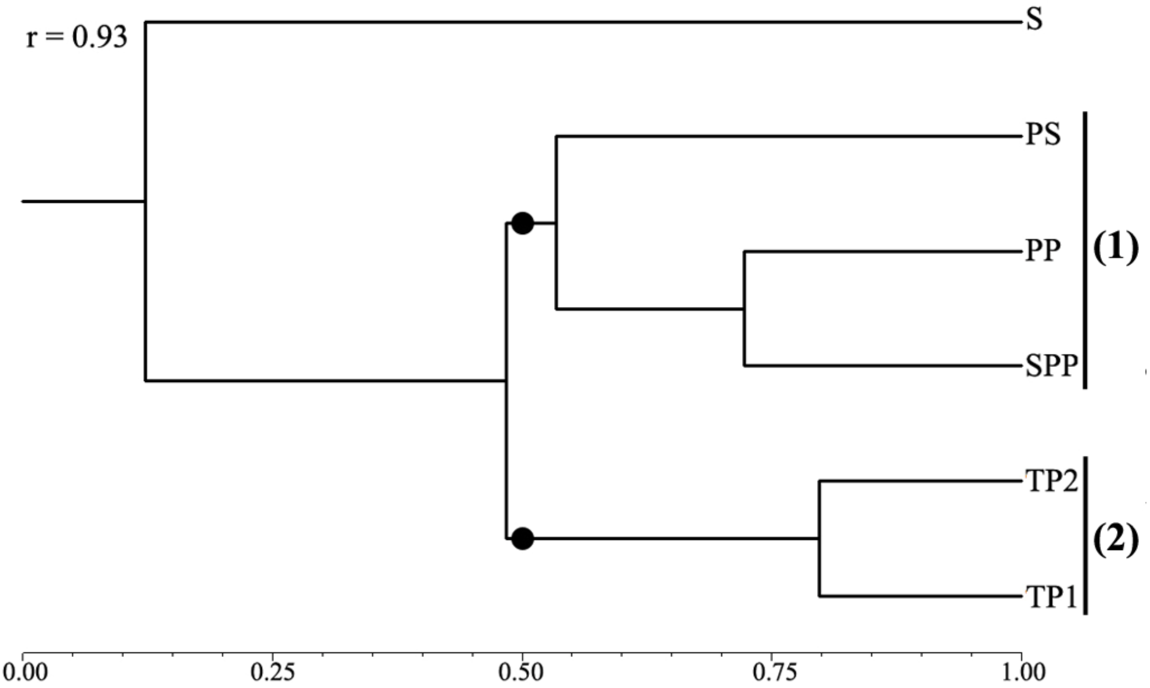
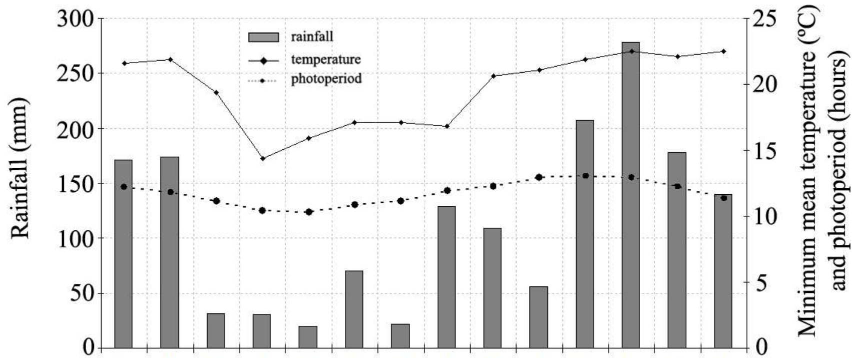


Figure 1. Similarity analysis of the six breeding habitats, considering the abundance of the anuran calling males at MDSP, São Paulo State, southeastern Brazil, from February 2006 to March 2007. r = Cophenetic Coefficient Correlation, S = Stream, PP = Permanent Pond, PS = Permanent Swamp, SPP = Semi-Permanent Pond, TP = Temporary Pond. Black circles represent break-points (similarity = 50%) for considering clusters (1) and (2).



	feb/06	mar/06	apr/06	may/06	jun/06	jul/06	aug/06	sep/06	oct/06	nov/06	dec/06	jan/07	feb/07	mar/07
Bufonidae														
Rhinella ornata						4	12							
Hylidae														
Dendropsophus minutus		2									30	11	8	
D. nanus	61	2						10	1		92	68	67	8
Hypsiboas albopunctatus									1				1	1
H. faber	9	9							1		5	24	16	14
H. raniceps	15							2	4	5	4	8	5	
Pseudis platensis											1			
Scinax berthae	20	11												
S. fuscomarginatus											35	25	20	
S. fuscovarius	5							2			27	22	1	
S. similis		1									70			
Trachycephalus venulosus									1	7	4			
Leiuperidae														
Eupemphix nattereri								6						
Physalaemus cuvieri	58	9						15			35	109	84	
Leptodactylidae														
Leptodactylus fuscus	1						1	4	11	10	36			
L. mystaceus									5	1	9	2		
L. mystacinus						4	13	15	4	4	12			
L. cf. *ocellatus*												1		
L. podicipinus	45							2	3	1	5	16	24	
Microhylidae														
Chiasmocleis albopunctata	2	1									20			
Elachistocleis bicolor	20	5									15	1		
Total Richness	10	8	0	0	0	2	3	8	9	6	16	11	9	3
Total Abundance	236	40	0	0	0	8	26	56	31	28	400	287	226	23

Figure 2. Temporal occurrence of calling males from 21 species in the MDSP, São Paulo State, southeastern Brazil, and climate data (rainfall, temperature, and photoperiod) from February 2006 to March 2007.

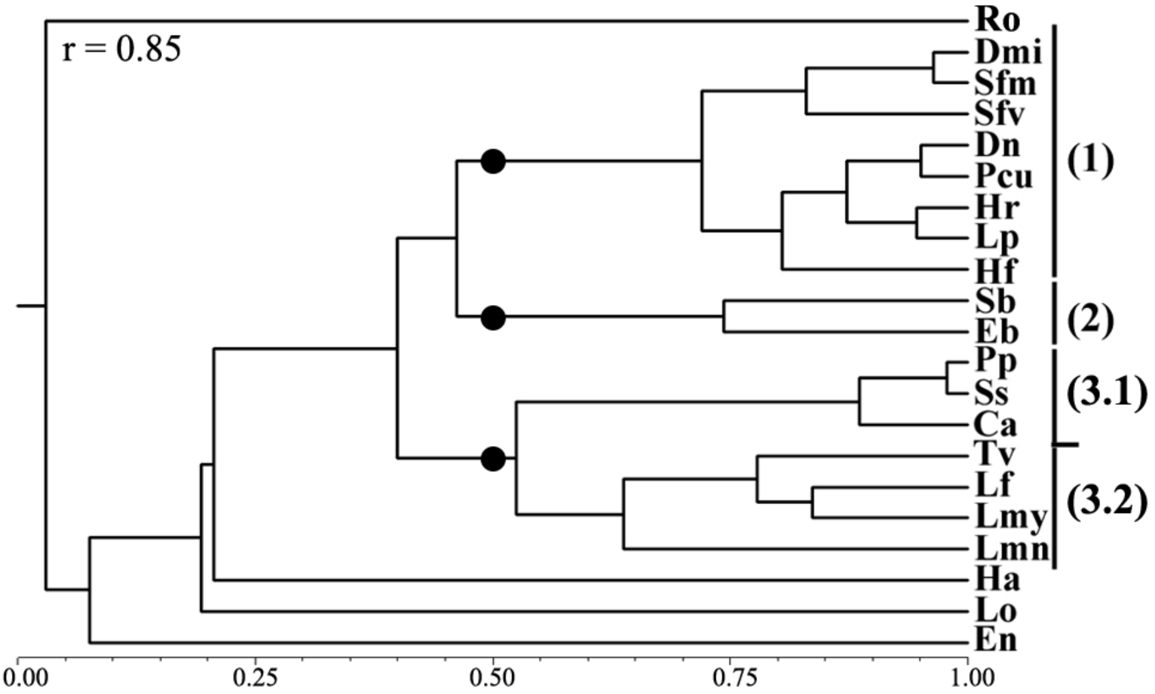


Figure 3. Similarity among temporal occurrence of anuran calling males from MDSP, São Paulo State, southeastern Brazil, from February 2006 to March 2007. r = Cophenetic Coefficient Correlation; black circles represent break-points (similarity = 50%) for considering clusters (1), (2), and (3). Ca = *Chiasmocleis albopunctata*, Dmi = *Dendropsophus minutus*, Dn = *D. nanus*, Eb = *Elachistocleis bicolor*, En = *Eupemphix nattereri*, Ha = *Hypsiboas albopunctatus*, Hf = *H. faber*, Hr = *Hypsiboas raniceps*, Lfu = *Leptodactylus fuscus*, Lmn = *L. mystacinus*, Lmy = *L. mystaceus*, Lo = *L.* cf. *ocellatus*, Lp = *L. podicipinus*, Pcu = *Physalaemus cuvieri*, Pp = *Pseudis platensis*, Ro = *Rhinella ornata*, Sb = *Scinax berthae*, Sfm = *S. fuscomarginatus*, Sfv = *S. fuscovarius*, Ss = *S. similis*, Tv = *Trachycephalus venulosus*.

CAPÍTULO 2

SPATIAL AND TEMPORAL DISTRIBUTION OF TADPOLE ASSEMBLAGES (AMPHIBIA, ANURA) IN A SEASONAL DRY TROPICAL FOREST OF SOUTHEASTERN BRAZIL

Spatial and temporal distribution of tadpole assemblages (Amphibia, Anura) in a seasonal dry tropical forest of southeastern Brazil

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ABSTRACT

In the present study we determined spatial and temporal distribution of tadpoles in six breeding habitats from Morro do Diabo State Park (MDSP), southeastern Brazil. We then tested whether the presence of tadpoles in each breeding habitat is different from a null model of random placement of species in those habitats. We also tested whether tadpole occupancy in a given breeding habitat is organized according to different ecomorphological guilds of tadpoles, and we analyzed spatial partitioning of tadpoles among breeding ponds through similarity analysis. For temporal analysis we analyzed temporal partitioning of tadpole presence for one year also using similarity analysis, and assessed what climatic variable better predicts tadpole temporal occurrence in the MDSP region, through regression analysis. Among tadpoles from 19 anuran species, distribution was different from a null model, but co-occurrence patterns did not differ among different guilds of tadpoles in the breeding habitats analyzed. However, breeding habitats with similar hydroperiods had similar species composition, which may be related to the reproduction patterns of species. Among the three climatic variables analyzed (rainfall, temperature and photoperiod), temporal occurrence of monthly tadpole richness and abuncance was correlated with rainfall and temperature. Most species were found only during the rainy season months, and overlap occurred within three groups of species. Thus, temporal distribution does not seem to be an important mechanism in species segregation at the MDSP, where the dry season is pronounced. In this case, spatial partitioning tends to be more important for species coexistence.

Key words: Brazilian amphibians, climatic relationship, phenology, spatial distribution, tadpole assemblages, seasonal forest.

Introduction

Tadpoles are known to form temporal assemblages in aquatic environments, which make the formation of stable long-term ecological associations impossible. Therefore, tadpoles became suitable models for examining ecological and evolutionary processes (Alford, 1999). Nonetheless, tadpoles are historically less studied than adult amphibians. Although tadpole research began in 18th century (see McDiarmid and Altig, 1999a for brief historic), ecological studies was not expressive into the literature before the 1960s (Alford, 1999). In Brazil, little attention is given to tadpoles, whereas most studies on natural history and ecology of anuran assemblages have focused on the adult phase (e.g., Pombal, 1997; Machado et al., 1999; Bertoluci and Rodrigues, 2002; Pombal and Gordo, 2004). Nonetheless, several studies of diverse field research have been performed on amphibian larvae during the last decade (see references in Fatorelli and Rocha, 2008).

One of the main goals of ecologists is to determine how species differ in their use of resources and to understand what determines the distribution, abundance, and diversity of organisms (Toft, 1985). Animals partition environmental resources in three basic ways: temporally, spatially and trophically (Pianka, 1973), but resource partitioning cannot be explained by any single factor. Rather, a complex array of abiotic and biotic effects interact, and makes species coexistence possible (Toft, 1985; Jakob, 2003). For instance, ecological studies have shown that tadpole assemblages are structured by species interactions (predation, competition, and interaction between their effects; Resetarits and Fauth, 1998; Eason and Fauth, 2001), environmental effects (e.g., vegetation cover, hydroperiod; Eterovick and Sazima, 2000; Werner et al., 2007), or even interactions between biotic and abiotic factors (e.g., the presence of aquatic vegetation as a factor in the reduction of tadpole predation; Kopp et al., 2006). Moreover, intrinsic factors (phylogenetic constraints) also influence tadpole distribution among their various environments (Eterovick and Fernandes, 2001; Fatorelli and Rocha, 2008). On the other hand, recent studies have proposed that communities can be organized only by stochastic process of birth, death, colonization, and extinction, which is not influenced by species trait, community composition, or environmental condition (see references in Tillman, 2004 and Chase, 2007). In this case, distinct tadpole assemblages are not found in sites with similar abiotic characteristics, and occurrence of any tadpole species in any single pond seems to be due to chance, i.e., may contain a large stochastic component (e.g., Heyer, 1973; Gascon, 1991; Wild, 1996).

Space and time are the most common dimensions analyzed in ecological studies of tadpole assemblages (e.g., Gascon, 1991; Rossa-Feres and Jim 1994, 1996; Eterovick and Barros, 2003; Jakob et al., 2003). For tadpoles, seasonal time is considered the most important dimension partitioned, followed by space and food (Toft, 1985). However, some studies have found that seasonal time was not important for explaining tadpole co-occurrence (Inger et al., 1986; Wild, 1996), and other have recorded high temporal overlap among tadpole assemblages (Rossa-Feres and Jim, 1994; Eterovick and Barros, 2003; Vasconcelos and Rossa-Feres, 2005). This high overlap on temporal occurrence seems to be related to the type of climate of each region studied (particularly rainfall), since unpredictability and inconsistency of rains in the beginning of wet season may limit temporal partitioning among amphibians species (Santos et al., 2007). However, few studies were performed in regions where rainfall is constant during the year (e.g., Inger, 1986; Both et al., 2009), which makes general comparisons difficult.

In the Brazilian Atlantic Forest Domain (sensu Ab’Saber, 1977), the Mesophitic Semideciduous Forest is the type of forest that suffered the most large-scale deforestation, due to its fertile soil and flat topography, which makes agricultural activities possible (Durigan and Franco, 2006). In the western region of São Paulo State, southeastern Brazil, Morro do Diabo State Park (MDSP) shelters one of the biggest remnants of this kind of vegetation, but no ecological study has been performed with amphibians in this area, although this region is considered a priority for herpetofaunal studies (MMA, 2002).

In this study, we determined the spatial and temporal occurrence of tadpoles from MDSP, and hypothesized that the tadpole assemblage would be spatially and temporally structured. For spatial distribution, we 1) tested whether the occurrence of tadpoles in each breeding habitat is different from a null model of random placement of species in those habitats; 2) tested whether tadpole occupancy in breeding habitats is organized according to different ecomorphological guilds of tadpoles; and 3) performed similarity analyses in order to assess how breeding habitats share different tadpole species. For temporal distribution, we hypothesized that temporal distribution of tadpole species varies through the year, and this variation is associated with climatic variables. We then assessed 1) how tadpoles partition temporal occurrence thorought the year; and 2) tested which climatic variable better predicts temporal occurrence of tadpoles at MDSP.

Material and Methods

Studied area and sampling procedures

Morro do Diabo State Park (MDSP) is located in the westernmost region of São Paulo state (southeastern Brazil), municipality of Teodoro Sampaio, Brazil. MDSP belongs to the Atlantic Forest Domain (Ab’Saber, 1977) and constitutes one of the largest remnants of Mesophytic Semideciduous Forest (encompassing about 34.000 ha) that remained after the process of degradation of the Atlantic Forest by human occupation (Faria, 2006a). In spite of the predominance of the Semideciduous Forest, MDSP also shelters some patches of Cerrado *sensu stricto* (Durigan and Franco, 2006), since it is located in a transitional zone between Atlantic and Cerrado Domains (Ab'Saber, 2003).

Weather in this region is characterized by a subtropical climate (Cwa of Köppen) with two distinct main seasons: a dry winter (generally from April to August) and a hot and wet summer (from September to March). Total annual rainfall accounts for 1,100 to 1,300 mm, and mean annual temperature is 22ºC, ranging from 10ºC to 35ºC (Faria, 2006b). Additional information concerning MDSP characterization and a map of the site is available in Santos et al. (2009) and Faria (2006a).

Field work was carried out at 11 breeding habitats (Table 1) with different physiognomic and structural characteristics: three streams, one semi-permanent pond, three permanent ponds, and four temporary ponds. These breeding habitats were monitored monthly from March 2006 to March 2007. Tadpole sampling was performed using a wire mesh dipnet (3 mm^2 mesh size), sweeping all available microhabitats for tadpoles (e.g., water column and edge of ponds with and without vegetation) from the floor to the surface (Vasconcelos and Rossa-Feres, 2005; Santos et al., 2009). The number of sweeps varied according to the size of the breeding habitat, since a large number of sweeps in larger breeding habitats reduces the risk of missing species that may have been concentrated in one area (Babbitt, 2005). Collected tadpoles were fixed in 10% buffered formalin and were deposited at the DZSJRP (UNESP/São José do Rio Preto, Brazil) Amphibian Collection (DZSJRP 1263.1 to 1316.6). Tadpoles were identified in the laboratory following Cei (1980) and Rossa-Feres and Nomura (2006).

Daily rainfall data was obtained from the meteorological station located inside of MDSP. Monthly mean of minimum temperature were taken from the Instituto Nacional de

Meteorogia (INMET) of Presidente Prudente, a city located about 100 km from the studied site. Finally, data on photoperiod were obtained from the Observatório Nacional Brasileiro (http://euler.on.br/ephemeris/index.php), based on the mean of the days that field work was carried out.

Statistical analyses

To begin, we tested if the occurrence of tadpoles in each breeding pond differed from a null model of random placement of species in breeding habitats. Then, a null model analysis was applied based on the observed and expected matricies of species occupation. The expected matrix was generated by the application of the C-score index (Stone and Roberts, 1990), in which observed rows (i.e. presence/absence of species) are fixed in the simulation, and columns (breeding habitats) are equally likely to be represented (Gotelli and Entsminger, 2001), considering 5,000 Monte Carlo simulations.

A Guild Structure Test (sensu Gotelli and Entsminger, 2001) was performed in order to test the hypothesis of whether tadpole occupancy in breeding habitats is organized according to different feeding/micro-spatial resource use by tadpoles. This analysis tests whether the mean co-occurrence index among different guilds is larger or smaller than a null model random distribution of species (Gotelli and Entsminger, 2001). Thus, tadpole guilds were determined according to McDiarmid and Altig (1999b) and Rossa-Feres and Nomura (2006), but *Dendropsophus nanus* and *Elachistocleis bicolor* were not considered in the analysis because the former species is the single representatives of macrophagous guild, and *E. bicolor* is the single representative of suspension feeder guild in the area studied. Consequently, two guilds (benthic and nektonic) were considered for tadpoles from MDSP (see Rossa-Feres and Nomura, 2006 to check the guild of each species). The mean occurrence index among guilds was then tested, and a presence/absence matrix of tadpole occupancy and their respective guilds was compared 1,000 times by Monte Carlo permutation with a null model matrix, generated by C-score index of co-occurrence (sensu Stone and Roberts, 1990), using the EcoSim software (Gotelli and Entsminger, 2001).

Analyses of tadpole habitat occupancy were performed qualitatively and quantitatively. Presence/absence of tadpoles in each breeding habitat was analyzed using the Jaccard coefficient (C_J) (Magurran, 1988). The beta diversity between pairs of compared breeding habitats was considered high when $C_J \leq 0,50$. Tadpole abundance of each species was used to calculate the Morisita-Horn index of similarity (Krebs, 1999). Before the analysis, we $\log_{(X+1)}$ transformed the total abundance of each tadpole, in order to downweight the contributions of quantitatively dominant species (Zar, 1999). A subsequent cluster analysis (unweighed mean method, UPGMA) was applied in the resultant matrix, and clusters were considered when similarity was ≥ 50%. A Cophenetic Correlation Coefficient (r) was calculated in order to verify how much the resulting graph of cluster analysis represents the original similarity matrix, where $r \geq 0.9$ represents a very good fit, 0.9 – 0.8 represents a good fit, 0.8 – 0.7 represents a poor fit, and $r < 0.7$ represents a very poor fit (Rohlf, 2000).

Temporal occurrence of species was monthly considered for the abundance of species in all breeding habitats studied, and species were then compared by the application of Morisita-Horn index of similarity (Krebs, 1999). Before the analysis, data were also $\log_{(X+1)}$ transformed, and a subsequent cluster analysis was applied (UPGMA) in the resultant matrix. Clusters were also considered when similarity was ≥ 50%, and a Cophenetic Correlation Coefficient was also calculated, in order to verify how much the resulting graph of cluster analysis represents the original similarity matrix (Rohlf, 2000).

In order to test whether climatic variables predict monthly species richness and abundance of tadpoles, a linear regression analysis between climatic data (rainfall, temperature, and photoperiod; independent variables) and monthly species richness and abundance (dependent variable) was performed (Zar, 1999). For this analysis, dependent and independent variables were $\log_{10}$ tranformed (Zar, 1999), and the model was submitted to a backward stepwise procedure.

Results

Tadpoles from 19 species and five families were recorded in the 11 studied breeding habitats (Table 2). Tadpole distribution among breeding habitats was different from a random occupancy (mean of observed C-score index = 3.43; mean of simulated C-score index = 4.00 ±0.05; p = 0.015). However, co-occurrence patterns of distribution were not organized according to the different guilds of tadpoles in the breeding habitats analyzed (mean of observed C-score index = 3.36, mean of simulated C-score index = 3.48, p = 0.405), which means that tadpole guild occupancy in the breeding habitats was more similar to a random placement of species than to a structured guild assemblage.

Species richness varied from two (in the Streams) to 12 (in the Semi-Permanent Pond) (Table 2). High beta diversity was found among breeding habitats (similarity values lower than 50% for 49 out of the 55 combinations between pairs of breeding habitats) (Table 3). The similarity analysis of breeding habitats using the abundance of tadpoles resulted in four clusters, made up of: 1) permanent lotic breeding habitats (S1, S2, and S3), which sheltered only two species (*Rhinela ornata* and *Hypsiboas albopunctatus*); 2) permanent lentic breeding habitats (PS and PP2), which sheltered some species with similar abundance patterns (e.g., *R. schneideri*, *H. raniceps*, and *Scinax fuscomarginatus*); 3) permanent and semi-permanent lentic breeding habitats (PP1 and SPP), which sheltered other species with similar abundance patterns (e.g., *H. faber* and *Physalaemus cuvieri*); and 4) temporary lentic breeding habitats (TP1 and TP2), which sheltered fewer species than the permanent ones, but with similar abundance of *Physalaemus cuvieri* (Figure 1).

Although most species occur only during the rainy season months, temporal distribution analyses showed partitioning among four clusters of species (Figure 2): 1) tadpoles that occurred in the first months of rainy season, but with highest abundance in September 2006: *Rhinella schneideri* and *Leptodactylus fuscus*; 2) tadpoles that were more abundant in December 2006 (*Eupemphix nattereri*, *Leptodactylus mystacinus*, and *Trachycephalus venulosus*); 3) species that occurred preferentially in the middle of the rainy season (January 2007: 3.1 - *Elachistocleis bicolor*, *Leptodactylus ocellatus*, and *Scinax similis*) and also occurred up to the end of the rainy season (February and March 2007: 3.2 - *Dendropsophus minutus*, *Dendropsophus nanus*, *Hypsiboas raniceps*, *Leptodactylus podicipinus*, *Physalaemus cuvieri*, *Scinax fuscomarginatus*, and *Scinax fuscovarius*); and 4) tadpoles that occurred throughout the period studied (*Hypsiboas albopunctatus* and *H. faber*).

Among the three climate variables analyzed, the regression model retained only temperature as a predictor for tadpole temporal occurrence (adjusted $r^2 = 0.674$; $F_{(1,11)} = 25.75$; $p = 0.000$; Beta coefficient of temperature = 0.84, $p = 0.000$). However, the regression model retained only rainfall when monthly abundance of tadpoles was considered (adjusted $r^2 = 0.523$; $F_{(1,11)} = 14.18$; $p = 0.003$; Beta coefficient of rainfall = 0.75, $p = 0.003$). Therefore, the highest abundance and species richness were recorded during the months with the highest values of precipitation and temperature (Figure 3). Only two species (*Rhinella ornata* and *Scinax berthae*) occurred preferentially during the dry/cold season (from April to August) (Figure 3).

Discussion

A random species distribution could be related to the Hubbell's Neutral Theory, which predicts that patterns of distribution is driven by stochastic drift densities of competitively identical species, and is not related to species traits or environmental conditions (for more details see Tilman, 2004 and Chase, 2007). Unlike random occupancy, distribution of tadpole assemblages in the present study differed among the 11 breeding sites. Various studies have demonstrated that tadpole assemblages (species composition and richness) are determined by deterministic processes, such as biotic factors (e.g., predation and competition: Resetarits and Fauth, 1998; Eason and Fauth, 2001) and abiotic factors (e.g., hydroperiod, canopy cover, and water flow: Eason and Fauth, 2001; Eterovick and Sazima, 2000; Werner et al., 2007). However, Wild (1996) found that tadpole assemblages from Cuzco Amazónico, Peru, may contain a large stochastic component regarding differential species occupancy in ponds. In the present study we tested whether species distribution was related to guild structure of tadpoles, which was not recorded herein. In fact, it was not expected because spatial distribution of tadpoles and their temporal patterns of occurrence result from the spatial and temporal distribution of reproductive effort by adult frogs, and adults may respond to many factors apart from the ecological requirements of their larvae (Alford, 1999). Guild structure, however, may play an important role in microhabitat partitioning within breeding habitats, since different use of microhabitat (e.g., Heyer, 1973; Kopp and Eterovick, 2006) may be due to specialized feeding habitats and adaptations of body morphology of tadpoles (Alford, 1999). However, morphology alone did not explain overlap in microhabitat use among tadpoles from different ecomorphological guilds in streams at the Serra do Cipó, southeastern Brazil (Eterovick and Barros, 2003). In this case, overlap in microhabitat use among tadpoles may be a result of behavioral plasticity (Eterovick and Barros, 2003), since differential microhabitat use within a species can be related to ontogenetic changes in tadpole development (Wild, 1996).

Although some overlap exists, partitioning among species (or groups of species) for habitat use has been recorded among tadpole assemblages in various studies (Gascon, 1991; Rossa-Feres and Jim, 1996; Santos et al., 2007; present study). In this study, partitioning is exemplified by the high beta diversity among breeding habitats (i.e., the fewer species that different assemblages share, the higher beta diversity is, sensu Magurran, 1988). In addition, similarity analysis of the abundance of tadpoles in each breeding habitat clustered ponds with similar characteristics (lotic, permanent, and temporary lentic habitats). Thus, the assemblages studied seem to be structured according to the physiognomic and structural characteristics of breeding habitats. The lotic breeding habitats sheltered only two species (*Rhinella ornata* and *Hypsiboas albopunctatus*), which are often associated with lotic habitats in other areas (e.g., Brasileiro et al., 2005; Vasconcelos and Rossa-Feres, 2005; Zina et al., 2007). The lowest species richness recorded in these habitats at MDSP has been previously recorded in various studies (e.g., Gascon, 1991; Rossa-Feres and Jim, 1996; Brasileiro et al., 2005; Vasconcelos and Rossa-Feres, 2005), which can be related to three non-exclusive hypotheses (Gascon, 1991): absence of tadpole adaptations to deal with flowing water, high predator pressure from fish, and historical evolutionary constraints of species.

Tadpoles in lentic breeding habitats in the MDSP seem to occur according to the pattern of reproduction exhibited by the species and hydroperiod of ponds. Gascon (1991) and Both et al. (2009), while studying tadpole assemblages in the Central Brazilian Amazon Forest and in the Pró-Mata reserve (southern Brazil), respectively, found that variations in tadpole occurrence among breeding habitats was partially related to the hydroperiod of ponds. In the same way, we recorded that tadpoles occurring preferentially in months of rainy season (e.g., *Dendropsophus minutus*, *Hypsiboas faber*, and *Scinax fuscovarius*) also occurred only in permanent and semi-permanent ponds. These species can be characterized as prolonged breeders (sensu Wells, 1977), since tadpoles in early developmental stages (stage 25 – 28, sensu Gosner, 1960), which represent a recent reproduction event, occurred at least in three months of the period studied (TSV and TGS, unpublished data). On the other hand, the presence of some explosive breeding species (sensu Wells, 1977; *Elachistocleis bicolor* and *Scinax berthae*) occurred preferentially in temporary ponds, where tadpoles in early developmental stages occurred only in the month immediately after heavy rains (TSV and TGS, unpublished data).

The highest species richness in the semi-permanent pond seems to agree with the intermediate-disturbance hypothesis (Connell, 1978). In fact, species richness patterns observed in the present study agree with Heyer et al. (1975), who proposed a model to explain tadpole communities across a hydroperiod gradient. To summarize, the model predicts that species richness would increase from ephemeral to temporary ponds, and decrease from temporary to permanent ponds, because some species can be excluded by fish predation. Werner et al. (2007) also found that larval amphibian richness in Michigan, USA, was higher in ponds with longer hydroperiods than in shorter and permanent ones. In the present study, temporary breeding ponds had lower species richness than permanent and semi-permanent ones, and kept water for a relatively short period (from October 2005 to March 2007, temporary breeding habitats kept water for a maximum of three months; TSV personal communication), which could be classified as ephemeral ponds, as proposed by Heyer et al. (1975). Similarly, Babbitt et al. (2003) and Babbitt (2005) found that ephemeral ponds (wetlands with a short hydroperiod: inundated < 4 months) in New Hampshire, USA, had significantly lower species richness than wetlands with an intermediate-long hydroperiod. However, the Semi-Permanent Pond did not dry up completely during the period studied, but water volume was reduced by about 90% of its total volume (including reduction of predator fish densities; TSV and TGS personal communication). This hydroperiod dynamic could be classified as an intermediate point between “r” and “k” selection (sensu Pianka, 1970), which should have led to the occurrence of both prolonged (e.g., *Hypsiboas faber*) and explosive breeders (e.g., *Elachistocleis bicolor*), resulting in a high species richness at this pond.

According to Toft (1985), temporal partitioning (specifically seasonal time) is the most important dimension partitioned by amphibian larvae. In the present study, the occurrence of most species was restricted to the rainy season, and partitioning was observed among three groups of species. However, overlap occurred within groups, mainly among species that occurred after heavy rains of January 2007 (ten species in the third group of Figure 3). A pronounced dry season, unpredictability, and inconsistency of rains in the beginning of the wet season were considered important factors limiting temporal partitioning in open area tadpole assemblages in southeastern Brazil (Santos et al., 2007). Similarly, wet season began in September 2006 in the present study, but heavy rains that effectively filled up temporary ponds and stimulated calling activities of most species occurred only in December 2006. Since the timing of frog reproduction determines the temporal distribution of tadpoles within sites (Alford, 1999), the unpredictability and inconsistency of rains may have restricted temporal occurrence of tadpoles in this study.

Therefore, temporal partitioning does not seem to be as important as spatial partitioning was for tadpoles at MDSP. Similar results for temporal occurrence were also recorded for tadpole assemblages in regions with distinct dry and wet seasons (Rossa-Feres and Jim, 1994; Wild, 1996; Eterovick and Barros, 2003; Vasconcelos and Rossa-Feres, 2005). On the other hand, Torres-Orozco et al. (2002) found temporal segregation in a tadpole assemblage in Mexico, where rainfall regime is higher than that recorded at MDSP. However, in this case, a much lower number of species (six species) was recorded, which suggests unsaturation at the tadpole assemblage studied by Torres-Orozco et al. (2002).

Although different cues are used by different species for the onset of reproduction (Gascon, 1991), only temperature was correlated with monthly richness and only rainfall was correlated with monthly abundance of tadpoles at MDSP. Rainfall and temperature have long been considered to be determinant factors for the regulation of breeding activities of tropical and subtropical amphibian assemblages (e.g., Aichinger, 1987; Duellman and Trueb, 1994; Vasconcelos and Rossa-Feres, 2005; Conte and Rossa-Feres, 2006), which is commonly related to the unique physiological and reproductive features of amphibians (Duellman and Trueb, 1994). However, temperature has long been considered to play a secondary role in the regulation of reproductive activities in tropical regions (Heyer, 1973), since it is probably correlated with rainfall occurrences, mainly in regions with climatic seasonality (Vasconcelos and Rossa-Feres, 2005; Santos et al., 2007). Temperature appears to be more determinant for temporal occurrence of tadpole assemblages in regions where rainfalls are evenly distributed through the year, such as the Brazilian temperate areas (Both et al., 2009). Although the photoperiod has received little attention in phenological studies, this abiotic factor also influences breeding activities of some amphibian species (e.g., Hatano et al., 2002). In a subtropical wet region in southern Brazil, Both et al. (2008) found a strong correlation only between the photoperiod and amphibian species richness. Both et al. (2008) argue that the photoperiod can be an important cue for environmental conditions suitable for reproduction (e.g., higher temperatures for calling activities and/or embryonic and larval development), especially for those species from temperate zones where variations in photoperiod and temperature are important for breeding activity of species (see references in Both et al., 2008).

Conclusion

Our results indicate that temporal distribution does not seem to be an important mechanism in species segregation, in which the dry season is pronounced. In this case, spatial partitioning tends to be more important for species coexistence. Thus, differential occupancy of breeding habitats by tadpoles is especially important for conservation purposes at MDSP, because it means that many different kinds of breeding habitats (e.g., streams, permanent, and temporary ponds) should be considered in the development of an effective safeguard for all amphibian species at MDSP. Since spatio-temporal patterns rely on the maintenance of species diversity of pond-breeding anurans (Both et al., 2009), temporal occurrence of tadpoles should also be considered for conservation purposes, because the hydroperiod of ponds depends on rainfall regime, as well as on the occurrence and abundance of tadpoles that were influenced by variations of temperature and rainfall through the year.

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Table 1. Main characteristics of the 11 studied breeding habitats of amphibians from MDSP, São Paulo State, Brazil. PP = Permanent Pond, PS = Permanent Swamp, S = Stream, SPP = Semi-Permanent Pond, TP = Temporary Pond.

	Geographic coordinates	**Total area**	**Hydroperiod**	**Surrounding environment**
PP1	22°22’10.2’’S; 52°19’43.0’’W	2000m^2	Permanent	Forest edge
PP2	22º27’03.7’’S; 52º20’43.3’’W	10000m^2	Permanent	Forest edge
PS	22°37’01.0’’S; 52°10’08.8’’W	900m^2	Permanent	Open area
S1	22°36’16.3’’S; 52°18’04.2’’W	2655m^2	Permanent	Forest
S2	22º36’16.2’’S; 52º18’00.8’’W	1065m^2	Permanent	Forest
S3	22º28’30.8’’S; 52º20’30.9’’W	1350m^2	Permanent	Forest
SPP	22º32’43.7’’S; 52º14’02.9’’W	900m^2	Semi-permanent	Forest edge
TP1	22º37’02.2’’S; 52º10’01.4’’W	300m^2	Temporary	Forest
TP2	22º37’06.8’’S; 52º10’05.9’’W	100m^2	Temporary	Open area
TP3	22º37’10.5’’S; 52º09’55.8’’W	3500m^2	Temporary	Forest
TP4	22º37’07.8’’S; 52º10’01.9’’W	702m^2	Temporary	Open area

Table 2. Spatial occupancy and ecomorphological guild (sensu Rossa-Feres & Nomura 2006) of tadpoles from MDSP, São Paulo State, Brazil. S = Stream, PS = Permanent Swamp, PP = Permanent Pond, SPP = Semi-Permanent Pond, TP = Temporary Pond, B = benthic, Nt = neustonic, N = nektonic, M = Macrophagous; SF1 = suspension feeder (Type 1).

	Guild	S1	S2	S3	PS	PP1	PP2	SPP	TP1	TP2	TP3	TP4
Bufonidae												
Rhinella ornata	B	■	■	■								
R. schneideri	B/Nt				■		■	■				
Hylidae												
Dendropsophus minutus	N				■			■				
D. nanus	M				■	■	■	■		■	■	■
Hypsiboas albopunctatus	B	■	■	■								
H. faber	B					■		■				
H. raniceps	B				■		■			■	■	■
Scinax berthae	N								■		■	
S. fuscomarginatus	N				■		■					
S. fuscovarius	N				■	■		■				
Scinax similis	N				■			■				■
Trachycephalus venulosus	N							■				
Leiuperidae												
Eupemphix nattereri	B					■		■				
Physalaemus cuvieri	B				■	■	■	■	■	■	■	■
Leptodactylidae												
Leptodactylus fuscus	B					■						
L. podicipinus	B				■	■	■	■			■	
L.* cf. *ocellatus	B							■				
L. mystacinus	B									■	■	■
Microhylidae												
Elachistocleis bicolor	SF1							■	■		■	
Total species richness		2	2	2	9	7	6	12	3	4	7	5

Table 3. Beta diversity among pairs of breeding habitats of anurans from MDSP, São Paulo State, Brazil. High beta diversity are highlighted in Italics ($C_J \leq 0.50$). Number of shared species between breeding habitats is written in boldface. S = Stream, PS = Permanent Swamp, PP = Permanent Pond, SPP = Semi-Permanent Pond, TP = Temporary Pond.

	S1	S2	S3	PS	PP1	PP2	SPP	TP1	TP2	TP3	TP4
S1	*	100	100	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*
S2	**2**	*	100	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*
S3	**2**	**2**	*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*
PS	0	0	0	*	*33.33*	66.67	*50*	*9.09*	*30*	*33.33*	*40*
PP1	0	0	0	**4**	*	*30*	*46.15*	*11.11*	*22.22*	*27.27*	*20*
PP2	0	0	0	**6**	**3**	*	*28.57*	*15*	*42.86*	*44.44*	*37.5*
SPP	0	0	0	**7**	**6**	**4**	*	*15.38*	*14.29*	*26.67*	*21.43*
TP1	0	0	0	**1**	**1**	**1**	**2**	*	*16.67*	*42.86*	*14.29*
TP2	0	0	0	**3**	**2**	**3**	**2**	**1**	*	57.14	80
TP3	0	0	0	**4**	**3**	**4**	**4**	**3**	**4**	*	*50*
TP4	0	0	0	**4**	**2**	**3**	**3**	**1**	**4**	**4**	*

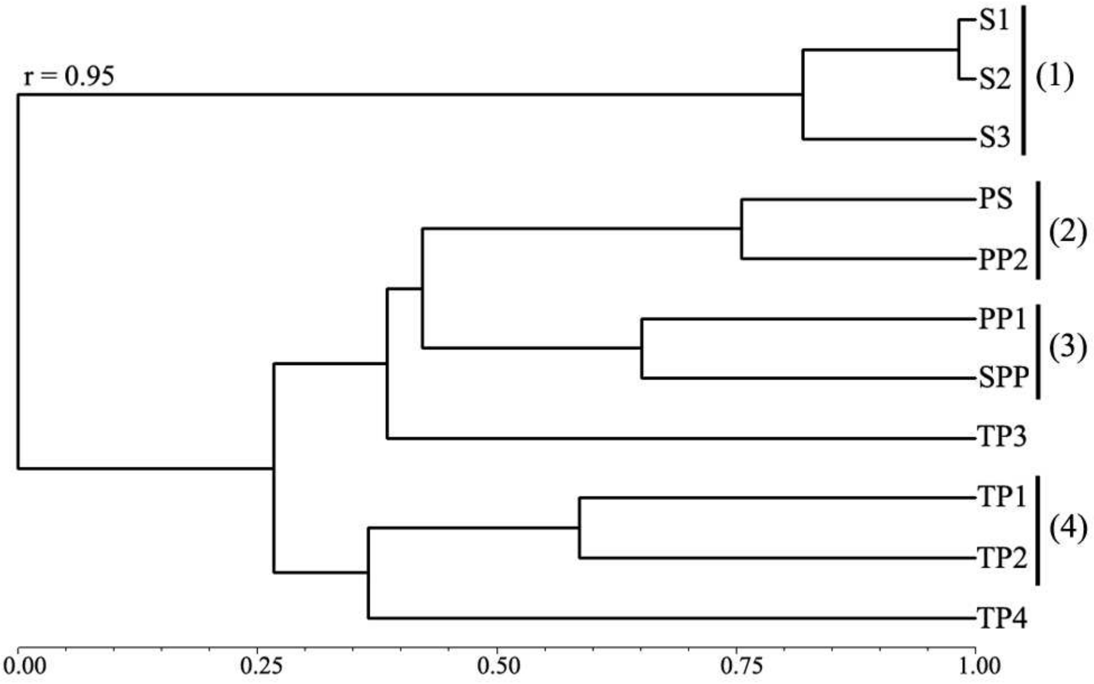


Figure 1. Similarity among the 11 breeding habitats studied at MDSP, São Paulo State, Brazil, according to the tadpole abundance. Numbers indicate clusters where similarity is over than 50%. r = Cophenetic Correlation Coefficient. Abbreviations of breeding habitats as in Table 1.

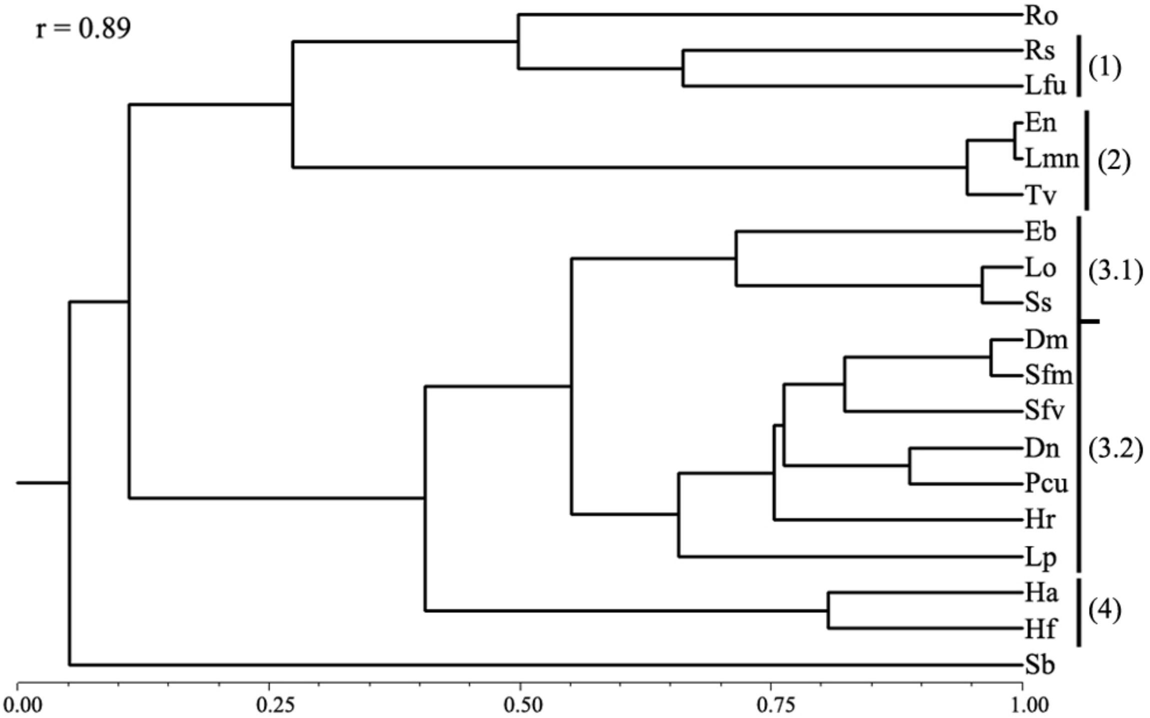
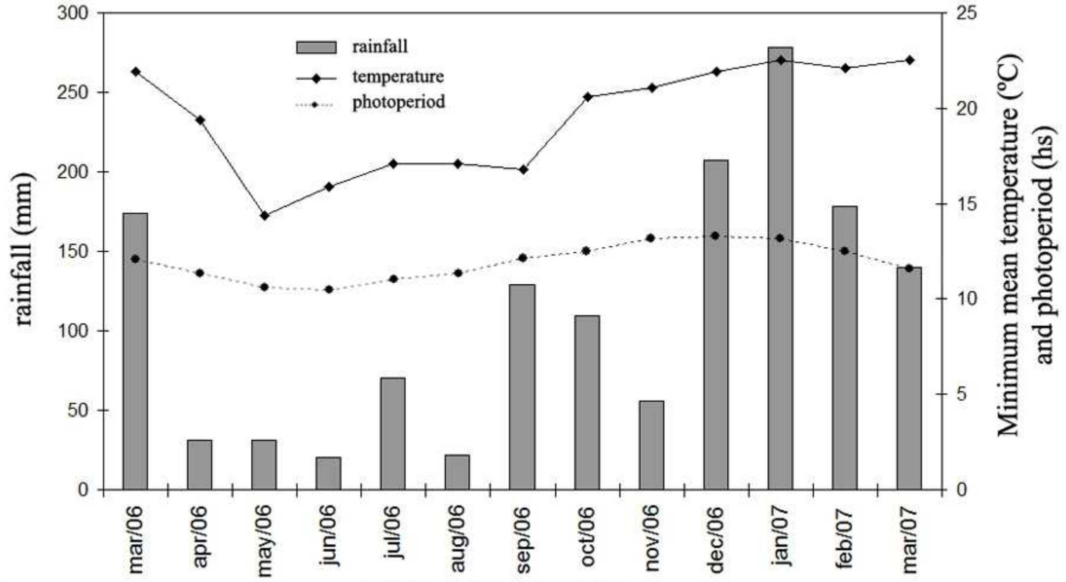


Figure 2. Similarity in the temporal occurrence of tadpoles from MDSP, São Paulo State, Brazil, from March 2006 to March 2007. Numbers indicate clusters where similarity is over than 50%. r = Cophenetic Correlation Coefficient. Dm = *Dendropsophus minutus,* Dn = *D. nanus,* Eb = *Elachistocleis bicolor*, En = *Eupemphix nattereri*, Ha = *Hypsiboas albopunctatus,* Hf = *H. faber,* Hr = *Hypsiboas raniceps*, Lfu = *Leptodactylus fuscus,* Lmn = *L. mystacinus,* Lo = *L.* cf. *ocellatus,* Lp = *L. podicipinus,* Pcu = *Physalaemus cuvieri,* Ro = *Rhinella ornata,* Rs = *Rhinella schneideri,* Sb = *Scinax berthae,* Sfm = *S. fuscomarginatus,* Sfv = *S. fuscovarius,* Ss = *S. similis,* Tv = *Trachycephalus venulosus*.



	mar/06	apr/06	may/06	jun/06	jul/06	aug/06	sep/06	oct/06	nov/06	dec/06	jan/07	feb/07	mar/07
R. ornata					111	337	107	137					
R. schneideri							1445	150					
D. minutus									1		26	16	6
D. nanus	1	3						12			24	14	10
H. albopunctatus	42	57	14	13	15	4	8	12	23	54	8		1
H. faber	57	72	102	77	51	9	27	8	16	7	101	176	450
H. raniceps								19	4	1	105	7	
S. berthae		16											
S. fuscomarginatus											6	2	2
S. fuscovarius								14		237	1044	468	48
S. similis	1										21		
T. venulosus										277			
E. nattereri								2		181			
P. cuvieri	72	20	14					46	13	2	391	275	91
L. fuscus							78	1		57			
L. mystacinus								3		71			
L. ocellatus											2		
L. podicipinus	105	1					122				43	520	133
E. bicolor	10	1									20	2	
Abundance	288	170	130	90	177	350	1787	404	57	887	1791	1480	741
Richness	7	7	3	2	3	3	6	11	5	9	12	9	8

Figure 3. Temporal occurrence and abundance of tadpoles from 19 species in the MDSP, São Paulo State, Brazil, and climate data (rainfall, temperature, and photoperiod) from March 2006 to March 2007.

CAPÍTULO 3

SIMILARITY OF TERRESTRIAL ANURAN (AMPHIBIA) COMPOSITION AMONG DIFFERENT PHYTOPHYSIOGNOMIES IN A MESOPHYTIC SEMIDECIDUOUS FOREST FROM SOUTHEASTERN BRAZIL

Similarity of terrestrial anuran (Amphibia) composition among different phytophysiognomies in a Mesophytic Semideciduous Forest from southeastern Brazil

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Abstract

We hypothesized that the composition of terrestrial anuran species vary according to the different selected phytophisiognomies of the Morro do Diabo State Park (MDSP), one of the largest remnants of Mesophytic Semideciduous Forest from southeastern Brazil. Thus, we compared the studied phytophysiognomies concerning their anuran species composition. We also tested if there are indicator species for these phytophysiognomies. Similarity analyzes showed a high beta diversity among the different phytophysiognomies, but it is rather a consequence of the low species richness recorded in the studied phytophysiognomies, instead of the different anuran species compositions expected among them. On the other hand, a higher similarity on species composition was found among the most preserved areas at MDSP, which is related to preferential habitat use of some species in these areas. Three species were indicative of the studied phytophysiognomies: *Rhinella ornata* as indicator of the Mature Forest, and *Eupemphix nattereri* and *Physalaemus cuvieri* as indicators of Forest in Advanced Regeneration Stage. We also discuss the efficiency of pitfall traps for capturing the anurans in the studied area.

Key words: Atlantic Forest domain; Cerrado; pitfall traps; seasonal forest; spatial distribution.

Introduction

Year by year studies on Brazilian amphibians has been arising in the most diverse research field (e.g., Eterovick and Fernandes, 2001; Aguiar Jr. et al., 2007; Zieri et al., 2007; Giovanelli et al., 2008; Santos et al., 2009). Description of new species has also been arising in the last years, since it had been described 97 new species between 1995 and 2005 in Brazil (Silvano and Segalla, 2005), and 59 new species from 2005 until today (SBH, 2009). Nevertheless, basic biology, natural history, ecology, and even geographic distribution remain unknown for the most Brazilian amphibian species (Silvano and Segalla, 2005). This becomes more worrying by the high rates of habitat destruction worldwide (Bush, 1997), which is the main threat to amphibians in Brazil (Silvano and Segalla, 2005).

From the northeastern to the southern Brazilian coastal range, Atlantic Forest domain (*sensu* Ab'Sáber, 1977) is considered one of the most rich and the most endangered biome in the world (Myers et al., 2000), which contains 405 anuran species that exhibit the most diversified number of reproductive modes in relation to other Brazilian biomes (Haddad & Prado, 2005). As a sub-domain of Atlantic Forest domain, the Mesophytic Semideciduous Forest, mainly characterized by the partial loss of leaves as a consequence of low rainfall during the winter (Veloso et al., 1991), experienced the most large scale deforestation among the Brazilian vegetation formation, due to its soil fertility (propitious for agricultural use) and flat topography that facilitates its use for cattle breeding (Faria, 2006a). Particularly in the westernmost region of São Paulo State, southeast Brazil, this deforestation was more intense, with the remaining vegetation in the region accounting for only 5% of its original distribution (São Paulo, 1999). Morro do Diabo State Park (MDSP) is located in this region, preserving the largest and most continuous remnant of Mesophytic Semideciduous Forest of São Paulo State, and is one of the four largest areas (over than 10,000 ha) that contains this kind of vegetation in Brazil (Faria, 2006a). However, only recently it was published the first study of amphibians from MDSP, where Santos et al. (2009) compared its species composition with anuran species from different localities of Brazil. Thus, there is no other study with amphibians at MDSP, which is considered insufficient known but with probable biological importance concerning amphibians and reptiles (MMA, 2000).

Since the MDSP has different vegetation landscapes (e.g., areas in different vegetation succession stage and a small patch of Cerrado, i.e., the Brazilian savanna), we hypothesized that the composition of terrestrial anuran species (captured by pitfall traps) vary according to the different selected phytophisiognomies of the MDSP. In this way, we aimed to compare the studied phytophysiognomies concerning their anuran species composition and we also tested if there are indicator species for theses studied areas.

Material and methods

Study area

Morro do Diabo State Park (MDSP) is one of the four largest continuous protected area (>10,000 ha) of Mesophytic Semideciduous Forest in the country, amounting for approximately 33,845 ha (Durigan and Franco, 2006), located in the westernmost region of São Paulo state in the southeastern of Brazil.

Climate is characterized as subtropical with dry winter and wet summer, and historical records indicate mean temperature of 22 °C and annual rainfall ranging from 1,100 to 1,300 mm (Faria, 2006b). Surrounding area is characterized by pasture for cattle breeding and agriculture activities, like soybean and sugarcane cultivation (Bedushi-Filho, 2006).

As a consequence of fragmentation effects by anthropic influence in a recent past, and particular local edaphic features, MDSP is characterized by a mosaic of forests in different regeneration stages, and also have a small patch of Cerrado *sensu stricto* in northern region of the park (Durigan and Franco, 2006). We performed anuran surveys in five phytophysiognomies (Figure 1), which are characterized in Table 1: Mature Forest with emergent trees (MF), Myrtaceae Forest without emergent trees (MyF), Forest in Advanced Regeneration Stage (FARS), Forest in Initial Regeneration Stage (FIRS), and Cerrado (CER).

Sampling procedures

We installed pitfall traps with drift fences (Corn, 1994; Cechin and Martins, 2000) in five phytophysiognomies of MDSP. Each phytophysiognomy contained three sets of traps, except for MF (the vegetation type with the most coverage area in MDSP) that contained six sets of traps. Each set was a line of ten burrowed buckets of 100 l, with the upper side at the same level of the ground, and 10 m apart from each other. The buckets were linked by a 90 cm high plastic fence, passing across the middle of each bucket, with the bottom edge embedded in the ground. Each set of trap was installed at a minimum distance of 100 m from the edge of the phytophysiognomy in order to minimize the edge effects on species composition (Primack and Rodrigues, 2002), and was also located at a minimum of 100 m from the closer set of trap. The traps remained opened for six consecutive days each month, from October 2005 to October 2006; and inspections for captured specimens were performed every 48 h, always in the morning. Thus, there were three inspections per month, and total sampling accounted for 1,728 sampling hours/bucket. Captured individuals were identified, collected (ten individuals per species), or marked by clipping one toe (adapted from Martof, 1953), and released near from the site of capture. Recaptured individuals were not considered in the subsequent samples. Voucher specimens were deposited at the DZSJRP (UNESP/São José do Rio Preto, São Paulo state, Brazil) and CFBH (UNESP/Rio Claro, São Paulo state, Brazil) anuran collections.

Statistical analyses

A species accumulation curve (collector curve) and five species richness estimators (based on presence/absence data: Bootstrap, Chao II, ICE, Jackknife I, and Jackknife II) were determined in order to evaluate the sampling efficiency of pitfall traps at MDSP (Santos, 2003), using EstimateS 8.0 software (Colwell, 2006).

Phytophysiognomy occupancy by terrestrial anurans of MDSP was performed qualitatively and quantitatively: presence/absence of anurans in each phytophysiognomy was analyzed by the Jaccard coefficient (C_J) (Magurran, 1988), and beta diversity between pairs of compared phytophysiognomy was considered high when $C_J \leq 0.50$; the $\log_{10}$ transformed data (for downweighting the contributions of quantitatively dominant species, *sensu* Zar, 1999) of total abundance of anurans in each phytophysiognomy was considered for Bray-Curtis index of similarity (Krebs, 1999). For testing the null hypothesis that there are no assemblage differences between the different phytophysiognomies (Clark and Gorley, 2006), based on the similarity of Bray-Curtis index of pairs of analyzed phytophysiognomies, One-Way Analysis of Similarity (ANOSIM) was performed considering 10,000 replicates (Clarke, 1993). According do Clark and Warwick (2001) and Clark and Gorley (2006), *R* statistics of ANOSIM, which varies from -1 to +1, is a very useful feature because it offers a direct interpretation of *R* as an absolute measure of the strength of the difference among groups. *R* will usually fall between 0 and 1, indicating some degree of dissimilarity between sites (Clark and Warwick, 2001). The null hypothesis is considered when *R* is approximately to zero, and negative values is unexpected, since it would correspond to a higher similarity across different phytophysiognomies, instead of higher similarities among replicates within a given phytophysiognomy (Clark and Warwick, 2001). Next, the pairwise ANOSIMs between all pairs of phytophysiognomies were also provided as a post-hoc test (Ryan et al., 1995). We represented the Bray-Curtis similarity matrix by the Non-Metric Multidimensional Scaling (NMDS) (Manly, 1994) and clusters were considered when similarity was $\geq 50\%$. We performed the Stress statistic (S) to measure the goodness of fit between the similarities in the NMDS 2-d ordination space and the original similarities contained in the original matrices (Clark and Warwick, 2001): $S < 0.05$ gives an excellent representation of the original similarity matrix; $S < 0.10$ corresponds to a good representation; and $S < 0.20$ still gives a potentially useful 2-dimensional picture. Similarity analyzes and Stress statistic were performed using NTSYSpc2.10 software (Rohlf, 2000) and ANOSIM was performed using PAST software (Hammer et al., 2001).

The Indicator Species Analysis (ISA) (Dufrêne and Legendre, 1997) was performed in order to test the presence of indicator species of the different phytophysiognomies studied at MDSP. The method combines information on the concentration of species abundance in a particular group (i.e., in a particular phytophysiognomy) and the faithfulness of occurrence of a species in a particular phytophysiognomy, considering monthly species abundance in each phytophysiognomy. It produces Indicator Values for each species in each group, varying from 0 (no indication) to 100 (perfect indication) (McCune and Mefford, 1999). Statistical significance of Indicator Values was tested using Monte Carlo permutation test (1000 replicates). ISA was performed using PC-ORD for Windows software (McCune and Mefford, 1999).

Results

Pitfall traps with drift fences captured 369 anuran specimens belonging to four families and nine species at the MDSP (Table 2). The species accumulation curve showed an ascendant format and did not reach stability (Figure 2). Species richness estimators showed that terrestrial species richness at MDSP tend to be higher than recorded herein (Figure 2). Species richness of studied phytophysiognomies varied from one species in the FIRS to five species (FARS, CER, and MyF). Four species were found in the MF (Table 2). Beta diversity was considered high ($C_J \leq 50$) among pairs of phytophysiognomies (Table 3), whereas only the pair MyF and CER showed low beta diversity.

Although species composition considering abundance of anurans was different among phytophysiognomies ($P = 0.0001$), the R statistics of ANOSIM was relatively low ($R = 0.31$). In fact, the ANOSIM pairwise comparisons evidenced that higher differences were found among those pairs containing FIRS (the highest R values), between FARS and MF, and between MF and CER (Table 4). The remaining R values were near to zero or even negative values (Table 4). The NMDS representation of the Bray-Curtis index showed one cluster containing CER, MyF, and MF, whereas FIRS and FARS showed lower similarities values between themselves and among the other phytophysiognomies (Figure 3).

ISA evidenced that there are three indicator species of the studied phytophysiognomies (Table 5): *Rhinella ornata* as indicator of MF, and *Eupemphix nattereri* and *Physalaemus cuvieri* as indicators of FARS. The remaining species were not indicator of any other studied phytophysiognomies (Table 5).

Discussion

All recorded species in the present study had already been recorded by visual and acoustic searches at breeding sites in the MDSP (see Santos et al., 2009 for a complete MDSP species list). Thus, pitfall traps with drift fences recorded only 32.14% (nine species) of the 28 known anuran species of MDSP. We expected that pitfall traps would be more effective, because this methodology is highly efficient for capturing terrestrial species, especially those not recorded in traditional visual methods (Corn, 1994; Cechin and Martins, 2000). Even though we consider only terrestrial species (those belonging to the families Bufonidae, Cycloramphidae, Leiuperidae, Leptodactylidae, and Microhylidae), pitfall traps captured 64.29% of the known 14 species. In fact, species accumulation curve did not reach stability, and richness estimators also showed that the number of species expected to be captured by pitfall traps is higher than the recorded herein. Both species accumulation curve and richness estimators point out that expected terrestrial species richness of MDSP is nearly to 14 species. The remaining species that were not recorded herein are: *Chiasmocleis albopunctata*, *Elachistocleis bicolor*, *Leptodactylus* cf. *ocellatus*, *L. chaquensis*, and *L. labyrinthicus*. With the exception of *Chiasmocleis albopunctata*, there is no plausible explanation for why these species were not recorded herein, since they were visually and/or acoustically recorded in adjacent areas associated to the sampled phytophysiognomies (T. S. Vasconcelos and T. G. Santos, unpublished data).

A high efficiency of pitfall traps in survey studies is usually reported for amphibians. For instance, pitfall and funnel traps with drift fences in clearcut areas with mixed pine-hardwood habitats in the Woodbury Tract, South Carolina (USA), was the most efficient methodology for surveying amphibians, capturing 12 out of the 13 recorded species, whereas other methods (coverboard and time-constrained searches) recorded only two species (Ryan et al., 2002). In the tropical rainforest and savanna woodland of the Offshore Islands of Sulawesi (Indonesia), pitfall traps and nocturnal searches were complementary methodologies for recording frog species (Gillespie et al., 2005). On the other hand, inefficiency of pitfall traps has also been recorded in survey studies. Pitfall traps installed in the grassland and secondary forest areas in the Muni Lagoon (Ghana) captured only two out of 13 anuran species, but in this case, field works accounted for only eight sampling days in this area (Raxworthy and Attuquayefio, 2000). As highlighted by Cechin and Martins (2000), pitfall traps with drift fences is not recommended for short-term studies, especially because most amphibian species present seasonal breeding activities throughout the year (Duellman and Trueb, 1994; Vitt and Caldwell, 2009), which can not be accomplished in short-term studies. Similarly to our study, Brasileiro et al. (2005) recorded 11 anuran species by pitfall traps in the Cerrado vegetation of Itirapina (São Paulo State, southeastern Brazil). In this area, Brasileiro et al. (2005) found 28 anuran species (15 terrestrial species), and none species was exclusive captured by pitfall traps. Reproductive modes of all species from MDSP are dependent on lentic or lotic water bodies (modes 1, 11, 13, 30, and modes 2, and 31, respectively *sensu* Haddad and Prado, 2005). Thus, species that are dependent on humid microhabitats for reproduction in forested areas, such as the genera *Brachycephalus* and *Ischnocnema*, with direct development of terrestrial eggs (*sensu* Haddad and Prado, 2005), were not recorded, mainly because of the hydrological deficit from March to October in the studied region (see complete discussion in Santos et al., 2009). Then, considering the high investments of time and money for installing and maintaining pitfall traps in the field (Corn, 1994; Cechin and Martins, 2000), we believe that the use of this methodology for survey purposes in seasonally dry areas (as MDSP and the Cerrado vegetation of Itirapina, studied by Brasileiro et al., 2005) should be disadvantageous for anurans, because the great majority of species tend to present reproductive modes associated to water bodies, whose traditional methodologies of visual and acoustic searches at breeding sites would be sufficient.

The high beta diversity among the different pairs of studied phytophysiognomies should be considered carefully in the present study. According to Magurran (1988), beta diversity is essentially a measure of how different (or similar) a range of habitats or samples are in terms of the variety of species found in them, where the fewer species that the different communities share, the higher the beta diversity will be. Actually, the high beta diversity in the present study is rather a consequence of the low species richness recorded in the studied phytophysiognomies, instead of the different anuran species composition expected among them. This is especially true for the beta diversity of pairs of phytophysiognomies that contain the FIRS, which presented only one species and the lowest values of Jaccard similarities. Even the analysis that consider the abundance of species was influenced by the absence of species in the FIRS, since the differences obtained by pairwise ANOSIMs post-hoc test were found in the pairs of phytophysiognomies containing FIRS (except for the pair FARS and MF).

The higher similarity on species composition was found among the most preserved areas of MDSP (CER, MF, and MyF), whereas forested areas were still more similar between them (MF and MyF). Dixo and Verdade (2006) found that areas with different conservation status have different anuran species compositions in an Atlantic rain forest locality in São Paulo State, southeastern Brazil, which can be associated to the conservation status of the studied areas and/or the closer geographic distance among areas (in Dixo and Verdade, 2006, areas with similar conservation status were nearest among themselves). In fact, these authors found that some species occur exclusively and/or preferentially in mature forest areas, which can be associated to the reproductive modes exhibited by these species, since the presumed high air humidity in mature forest may favours the occurrence of species that put terrestrial eggs. In the present study, the higher similarity between pristine forested areas is due to the occurrence of *Rhinella ornata*. Although *Rhinella ornata* occurred in the two most preserved areas of MDSP, this species was an indicative of the MF, breeding in the streams of the most preserved area of MDSP (Santos et al., 2009). Because this species is generally associated to forested areas along its geographical range (e.g., Bernarde and Anjos, 1999; Brasileiro et al., 2005; Pombal and Haddad, 2005; Bertoluci et al., 2007; Zina et al., 2007; present study), we can suppose that it had its natural occurrence adversely affected by the habitat loss in the northwestern region of São Paulo State (Santos et al., 2009). This statement can be supported by the absence of this species in strongly impacted areas in northwestern São Paulo State (Vasconcelos and Rossa-Feres, 2005; Santos et al., 2007; Silva et al., 2008) and because forest anurans with aquatic larvae are negatively affected by the disconnection of the forest remnants from their breeding sites, promoted by anthropic modifications (Becker et al., 2007).

Two Leiuperidae species (*Eupemphix nattereri* and *Physalaemus cuvieri*) were indicators of FARS at MDSP. These species are known to occur in natural open areas (e.g., Cerrado biome) or disturbed areas, and are tolerant to anthropic alterations (e.g., Brandão and Araújo, 1998; Colli et al., 2002; Vasconcelos and Rossa-Feres, 2005; Santos et al., 2007). In the area where pitfall traps were installed at MDSP, FARS is in touch with agricultural areas, and there are some breeding ponds along the boundaries of the studied phytophysiognomy where breeding of *Eupemphix nattereri* and *Physalaemus cuvieri* were documented from August 2006 to February 2007 (T. S. Vasconcelos and T. G. Santos, unpublished data). Thus, the association of these two Leiuperidae species to FARS can be additional examples of species that are successful colonizers in disturbed environments, as already documented for *Physalaemus cuvieri* and *Leptodactylus fuscus* in other Brazilian regions (Haddad and Prado, 2005).

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Table 1. Characterization of the studied phytophysiognomies where pitfall traps were instaled at MDSP, São Paulo State, southeastern Brazil.

Phytophysiognomies	Lines	Coordinates	Characteristics (*sensu* Durigan and Franco 2006)
Cerrado *sensu stricto*	L1	22°28’10.8”S; 52°20’28.5”W	Mainly characterized by the predominance of herbaceous, shrubby, and some small form of arboreal species, typically from Cerrado. The ground is partially covered by grass and herbaceous plant as ‘caraguatá’ (*Bromelia balansae*) and the Cerrado pineapple (*Ananas ananassoides*).
	L2	22°28’05.8”S; 52°20’28.2”W	
	L3	22°28’06.6”S; 52°20’32.8”W	
Forest in Advanced Regeneration Stage	L1	22°22'13.7"S; 52°19'35.5"W	It is a diversified forest with continuous canopy. Emergent trees are rare and there is a high vine concentration. Although there are some typical species of initial stage of regeneration, there are young individuals, typically from the most advanced regeneration stages.
	L2	22°22'15.4"S; 52°19'42.2"W	
	L3	22°22'17.0"S; 52°19'54.0"W	
Forest in Initial Regeneration Stage	L1	22°32'07.4"S; 52°15'59.7"W	Open area that is in natural process of secondary succession, mainly characterized by the predominance of ‘sapé’ (*Imperata brasiliensis*). The most abundant species are those whose seeds are dispersed by animals and wind (typical colonizers): *Gochnatia polymorpha*, *Platypodium elegans*, *Guarea guidonea*, and *Didymopanax morototonii*.
	L2	22°32'03.1"S; 52°15'58.5"W	
	L3	22°32'08.0"S; 52°15'58.7"W	
Mature Forest	L1	22°36'19.4"S; 52°17'58"W	Forest that is characterized by the partial loss of leaves, with big emergent trees (up to 40 m high) as ‘peroba’ (*Aspidosperma cylindrocarpon*), ‘cedro’ (*Cedrela fissilis*), ‘ipê-roxo’ (*Tabebuia heptaphylla*), and ‘ipê-amarelo’ (*Tabebuia ochracea*). These species are indicators of fertile soils, which stand out from the lower continuous canopy (approximately 15 m high).
	L2	22°36'27.3"S; 52°17'56.1"W	
	L3	22°36'38.8"S; 52°17'57.4"W	
	L4	22°36’20.4”S; 52°18’04.6”W	
	L5	22°36’25.4”S; 52°18’03.5”W	
	L6	22°36’38.0”S; 52°18’01.1”W	
Myrtaceae Forest	L1	22°28’36.5”S; 52°20’42.3”W	Characterized by low canopy, great luminosity, and ground covered by ‘caraguatá’ (*Bromelia balansae*). This phytophysiognomy seems to be associated to edaphic local features (low soil fertility or deficient drainages) and is composed by a mix of Cerrado and Mature forest vegetation species, with predominance of arboreal species of the family Myrtaceae.
	L2	22°28’36.5”S; 52°20’35.8”W	
	L3	22°28’28.7”S; 52°20’36.6”W	

Table 2. Anuran amphibians captured by pitfall traps in different phytophysiognomies at Morro do Diabo State Park, São Paulo state, southeastern Brazil. CER = Cerrado, FARS = Forest in Advanced Regeneration Stage, FIRS = Forest in Initial Regeneration Stage, MF = Mature Forest, MyF = Myrtaceae Forest.

	CER	**FARS**	**FIRS**	**MF**	**MyF**	**Total**
Bufonidae						
Rhinella ornata	1	0	0	17	15	**33**
Rhinella schneideri	4	11	2	8	12	**37**
Cycloramphidae						
Odontophrynus americanus	1	2	0	0	0	**3**
Leiuperidae						
Eupemphix nattereri	0	18	0	0	0	**18**
Physalaemus cuvieri	1	266	0	3	2	**272**
Leptodactylidae						
Leptodactylus fuscus	1	0	0	0	2	**3**
Leptodactylus mystaceus	0	0	0	1	0	**1**
Leptodactylus mystacinus	0	1	0	0	0	**1**
Leptodactylus podicipinus	0	0	0	0	1	**1**
Total abundance	**8**	**298**	**2**	**29**	**32**	**369**
Species richness	**5**	**5**	**1**	**4**	**5**	**9**

Table 3. Similarity among the five phytophysiognomies sampled at MDSP, São Paulo State, southeastern Brazil, considering species composition of terrestrial anurans (Jaccard coefficient). High beta diversity between combinations pairs are highlighted in Italics ($C_J \leq 50\%$).

	CER	MyF	MF	FARS	FIRS
CER	*	66.67	*50*	*42.86*	*20*
MyF	*	*	*50*	*25*	*20*
MF	*	*	*	*28.57*	*25*
FARS	*	*	*	*	*20*
FIRS	*	*	*	*	*

Table 4. Pairwise comparisons of ANOSIMs among the five studied phytophysiognomies of MDSP, São Paulo State, southeastern Brazil. In Italics are highlighted the pairs where differences were found between pairs of phytophysiognomies ($P < 0.05$). Bold numbers indicate R values of the test.

	CER	MyF	MF	FARS	FIRS
CER	-	0.641	*0.016*	0.161	*0.000*
MyF	**-0.025**	-	0.092	0.059	*0.000*
MF	**0.19**	**0.09**	-	*0.000*	*0.000*
FARS	**0.04**	**0.10**	**0.41**	-	*0.000*
FIRS	**0.56**	**0.53**	**0.64**	**0.90**	-

Table 5. Species Indicator Analysis (ISA) for spatial distribution of anuran species in the five studied phytophysiognomies from October 2005 to October 2006 at the MDSP, São Paulo State, southeastern Brazil. Groups: 1) Cerrado, 2) Myrtaceae Forest, 3) Mature Forest, 4) Forest in Initial Regeneration Stage, 5) Forest in Advanced Regeneration Stage. Indicator values (IV) and statistical significance (*P*). ns = *P*>0.05.

Species	Group	IV	*P*
Rhinella ornata	3	38.6	0.002
Rhinella schneideri	2	13.9	0.571
Eupemphix nattereri	5	50	0.000
Leptodactylus fuscus	2	5.6	1.00
Leptodactylus mystaceus	3	8.3	1.00
Leptodactylus mystacinus	5	8.3	1.00
Leptodactylus podicipinus	2	8.3	1.00
Odontophrynus americanus	5	11.1	0.492
Physalaemus cuvieri	5	97.8	0.000

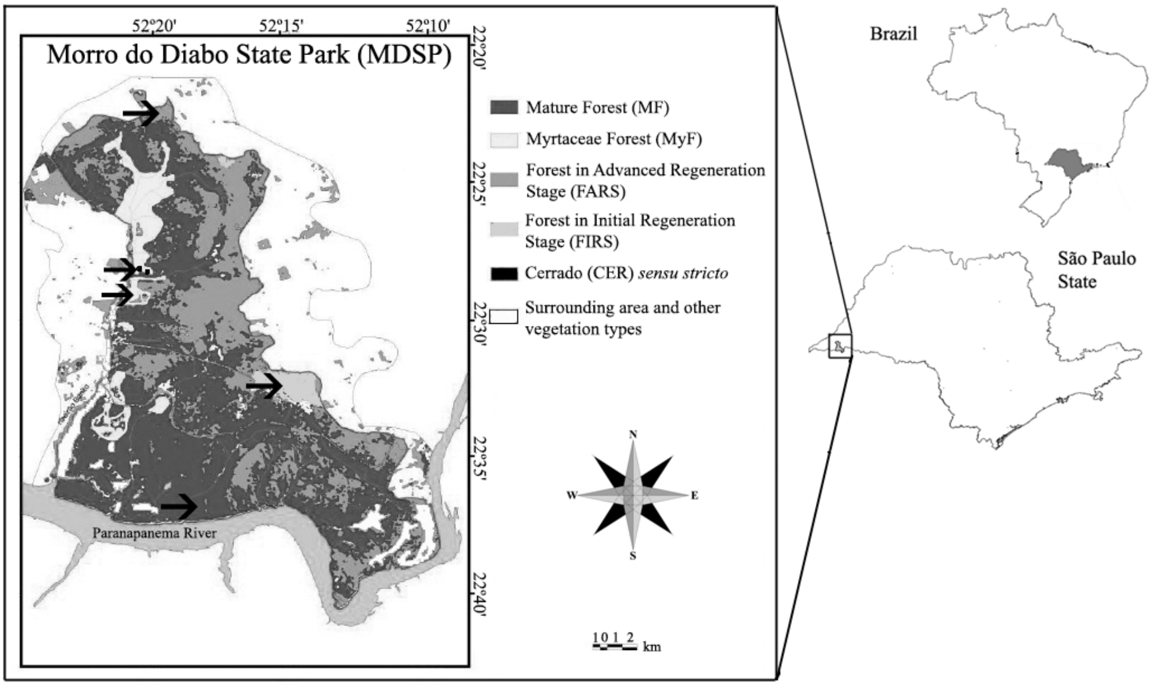

Figure 1. Location of Morro do Diabo State Park (MDSP) in São Paulo State (Brazil) and studied phytophysiognomies where pitfall traps were installed for anuran sampling. Arrows indicate where pitfall traps were installed in each studied phytophysiognomy. Modified from Durigan and Franco (2006).

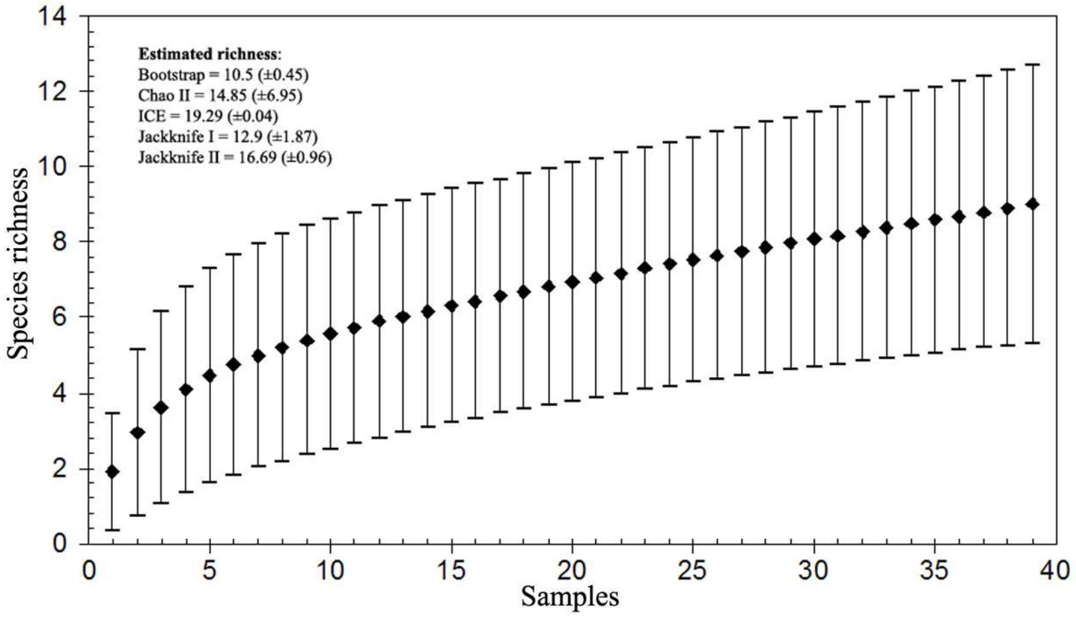

Figure 2. Species accumulation curve and richness estimators of terrestrial anurans recorded in five phytophysiognomies of MDSP, São Paulo State, southeastern Brazil, from October 2005 to October 2006. Central points are the mean cumulative curve, and the vertical bars indicate the respective variation around the mean (confidence interval of 95%).

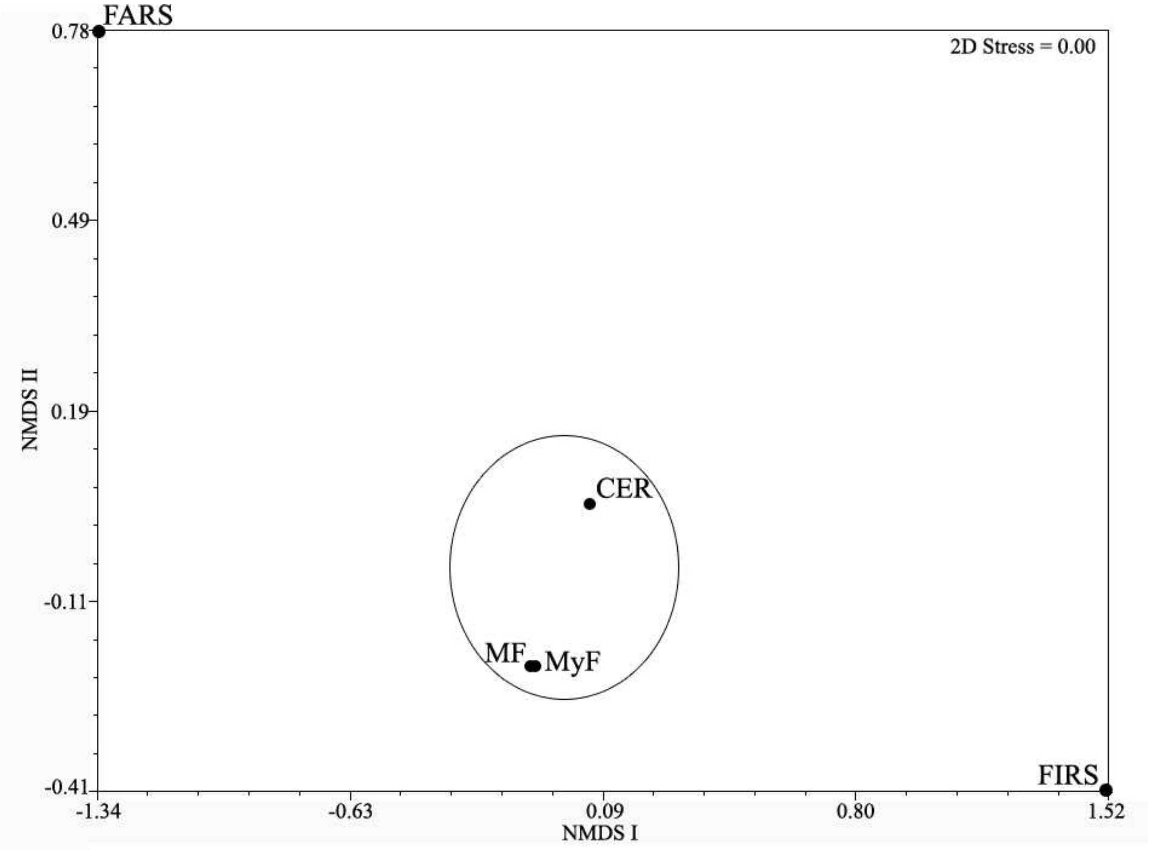

Figure 3. Similarity of studied phytophysiognomies concerning spatial distribution of terrestrial anurans of MDSP, São Paulo State, southeastern Brazil, collected from October 2005 to October 2006. The ellipse represents the cluster (similarity ≥ 50% between pairs of phytophysiognomies). CER = Cerrado, FARS = Forest in Advanced Regeneration Stage, FIRS = Forest in Initial Regeneration Stage, MF = Mature Forest, MyF = Myrtaceae Forest.

CAPÍTULO 4

INFLUENCE OF THE ENVIRONMENTAL HETEROGENEITY OF BREEDING PONDS ON ANURAN ASSEMBLAGES FROM SOUTHEASTERN BRAZIL

Influence of the environmental heterogeneity of breeding ponds on anuran assemblages from Southeastern Brazil

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Abstract

We hypothesized that the environmental heterogeneity of breeding ponds influences the species composition and species richness of anuran assemblages from southeastern Brazil, because it provides humidity, shelter and breeding microhabitats for anuran species, which can result in an increasing number of species in a given habitat. To begin, we tested whether the occurrence of anuran species in each breeding pond is different from a null model of random placement of species in those ponds. We then performed two tests to evaluate which of the five environmental descriptors of breeding ponds influence 1) the species composition; and 2) species richness. Species composition of the 38 breeding ponds was correlated with number of edge types, number of plant types along the edges of the breeding ponds, and the hydroperiod. Neither the percentage of vegetation cover on the water's surface nor the size of the breeding ponds were correlated with species composition. Only the number of edge types was correlated with species richness of breeding ponds. The correlation of three environmental descriptors with species composition and one environmental descriptor with species richness, and the high beta diversity among breeding ponds suggest that the analyses of environmental heterogeneity on species composition was more informative than was the analysis for species richness, because breeding ponds with similar species richness can have distinct species composition among them (high beta diversity).

Introduction

Anuran amphibians exhibit a wide variety of morphological structures, physiological mechanisms, and behavioral responses that enable them to occupy nearly all terrestrial habitats. However, most species inhabit regions that have high moisture levels and moderate to warm temperatures owing to their skin permeability and dependence on aquatic and terrestrial habitats during their life cycles (Duellman and Trueb 1994; Wells 2007). Thus, human impact on the environment makes amphibians one of the most vulnerable animal groups. Destruction of their habitats is documented as the main threat to this animal group in Brazil (Silvano and Segalla 2005). In forested areas, deforestation makes the environment drier and more seasonal, reducing the number of anuran species or sometimes eliminating those that depend on humid forest microhabitats (Haddad and Prado 2005). In addition, habitat disconnection caused by human activities in natural areas reduces population size and adversely affects the anuran richness in local assemblages that depend on breeding ponds for reproduction (Becker et al. 2007).

Because of the high dependence that anurans have on environmental quality, it has been demonstrated in some areas that abiotic factors (rainfall, temperature, and vegetation heterogeneity) have greater effects on the structure of anuran communities than biotic factors (competition and predation) (Parris 2004; Werner et al. 2007). The first studies that point out the importance of environmental heterogeneity in the structure of anuran assemblages are largely descriptive and did not test this prediction (e.g., Cardoso et al. 1989; Pombal 1997; Arzabe et al. 1998; Bernarde and Kokubum 1999). Today, owing to the development and availability of statistical softwares, several studies have effectively tested the prediction that environmental heterogeneity affects the structure of anuran assemblages. These studies also assess which environmental descriptors are most important to the assemblage (e.g., Parris and McCarthy 1999; Ricklefs and Lovette 1999; Parris 2004; Bastazini et al. 2007; Afonso and Eterovick 2007; Keller et al. 2009). However, most studies have shown divergent results concerning the influence of the environmental descriptors to a given anuran assemblage (e.g., the influence of the size of ponds on amphibian species richness; Parris and McCarthy 1999; Oertli et al. 2002; Afonso and Eterovick 2007). These divergent results may indicate that a single environmental descriptor has different effects in different anuran assemblages, and the particular characteristics of each locality need to be studied to assess which environmental descriptors have major importance. Thus, we hypothesized that the environmental heterogeneity of breeding ponds influences the species composition and species richness of anuran assemblages from southeastern Brazil, because it provides humidity, shelter, and breeding microhabitats for anuran species (Parris and McCarthy 1999; Haddad and Prado 2005; Afonso and Eterovick 2007), which can result in an increasing number of species in a given habitat. To begin, we tested whether the occurrence of anuran species in each breeding pond is different from a null model of random placement of species in those ponds. We then performed two tests to evaluate which of the five environmental descriptors of breeding ponds influence 1) the species composition and 2) species richness.

Material and methods

Study area and heterogeneity of breeding ponds. Four localities were selected in southeastern Brazil, where previous studies had been conducted using the same methodology, both for anuran sampling and to determine the heterogeneity of breeding ponds (Figure 1): Icém (Candeira 2007), Nova Itapirema (Vasconcelos and Rossa-Feres 2005), Morro do Diabo State Park (Santos et al. 2009), and Santa Fé do Sul (Santos et al. 2007). The municipalities of Icém, Nova Aliança, and Santa Fé do Sul are located in São Paulo State (northwestern region), whose climate is characterized by hot and wet summers (with the rainy season generally from September to March, accumulating 85% of the total annual rainfall of 1100-1250 mm of precipitation) and dry winters (generally from April to

August, accumulating the remaining 15% of total annual rainfall) (Barcha and Arid 1971). Morro do Diabo State Park (MDSP, Municipality of Teodoro Sampaio) is located in the westernmost region of São Paulo State, and is also characterized by two main seasons throughout the year (one hot and wet season from September to March and another cold and dry season from April to August), but frosts may occur during the coldest period of the year, and rainfall accumulates 1 370 mm annually (Faria 2006). In spite of these slight climate differences between MDSP (western São Paulo State) and other localities in northwestern São Paulo State, ecological processes in both regions are strongly driven by seasonal factors (Toby Pennington et al. 2000), which in turn influence the anuran species composition (see examples in Santos et al. 2009). Anuran species compositions among the selected localities are highly similar (Table 1), and most species are characterized by living in open areas, and are habitat generalist, tolerant to anthropic alterations, and exhibit unspecialized reproductive modes (Santos et al. 2009). In addition, although northwestern São Paulo State is highly fragmented by agricultural activities (PROBIO 1998; Durigan et al. 2007), both regions studied are within the Mesophytic Semideciduous Forest, a subtype of the Atlantic Forest domain (sensu Ab'Saber 1977), characterized by the partial loss of leaves as a consequence of low rainfall during the winter (Veloso et al. 1991).

Sampling procedures

Anuran sampling was performed using the "survey at breeding sites" method (sensu Scott Jr. and Woodward 1994) and by sampling tadpoles (Vasconcelos and Rossa-Feres 2005; Santos et al. 2007) for all breeding ponds. The sampling at each of the four locations was performed at least over the cycle of one year: every month during the dry season and every two weeks during the rainy season months (except in the MDSP, where sampling was monthly during the year). Thus, the number of samplings amounted to 18 in Santa Fé do

Sul (September/2003-August/2004), 19 in Icém (September/2004-August/2005), 19 in MDSP (September/2005-March/2007), and 25 in Nova Itapirema (January/2003-March/2004). Despite the lower sampling effort in the months of rainy season in MDSP compared with other locations, the applied methodology was efficient for recording the species at MDSP, as shown by the richness estimators (ICE, Boostrap and Jackknife I: 28 ± 0 species; sensu Santos et al. 2009).

Heterogeneity of breeding ponds

The sampled breeding ponds at these four locations have distinct structural (in terms of size and hydroperiod) and physiognomical characteristics (in terms of the types and quantity of vegetation inside and around the edges), which are representative of the different types of breeding ponds available for anurans in the studied region.

Thus, five environmental descriptors representing these structural and physiognomical characteristics were considered in order to assess the complexity of breeding ponds (Table 2). The five descriptors considered are as follows:

a) the number of plant types around the edge of breeding ponds, which varies from creeping vegetation to arboreal vegetation (important mainly as a calling site for perching species); b) the percentage of vegetation cover on the water's surface (which serves as shelter and foraging sites for tadpoles, as well as an important calling site for perching species and for species that call while floating on the water); c) the number of edge types, which vary between dry soil (commonly found in sloped edges, above the water level), humid soil (which has a fine layer of water on the soil), and flooded soil (which includes small pools of water, commonly found on flat edges). These edges are important as calling sites for terrestrial species, and were assessed up to five meters outside of the breeding ponds; d) the hydroperiod of breeding ponds, which varies from temporary pond to permanent pond. Although both permanent and semi-permanent categories are used for breeding ponds that did not dry up throughout the studied period, we considered semi-permanent ponds to be those that had their water volume reduced by at least 90% of their maximum volume. Thus, the semi-permanent ponds can be classified as an intermediate between permanent and temporary ones, because they do not dry up completely throughout the season, but may have their predator fish abundance strongly reduced at its lowest water volume (T. S. Vasconcelos and T. G. Santos, unpublished report); and e) the size of breeding ponds, categorized according to the distribution of sizes in a box-plot graphic (considering minimum and maximum values, the median value, and first and third quartiles, i.e. points that separate the lower 25% from the upper 75% values of ordered data set, and lower 75% from the upper 25% values, respectively) (Triola 1999; Zar 1999). As shown in Table 2, each breeding pond was characterized according to the details of each environmental descriptor, determined in the months during which breeding ponds retained their highest water volumes (generally in the middle of the rainy season), except for the hydroperiod. Breeding ponds were checked for standing water during each field work; thus, the hydroperiod at each pond had to be characterized after the studied period. The ordination procedure in ranks (sensu Zar 1999) was adopted following previous studies that analyzed the influence of habitat heterogeneity on open-area anuran assemblages (Vasconcelos and Rossa-Feres 2005; Candeira 2007; Santos et al. 2007), as data on an ordinal scale is highly applicable for assessing relative differences rather than quantitative differences, and for qualitative data as well (e.g., the number of edge types) (Zar 1999). Thus, the ordination procedure reduced the minor variations of the environmental descriptors, which come up when continuous variables are determined, because they can make it difficult to visualize a possible pattern.

Statistical analysis

We considered the species composition of anurans in the 38 analyzed breeding ponds. To begin, we tested whether the occurrence of anuran species in each breeding pond differed from a null model of random species placement in ponds. Then, a null model analysis was applied based on the observed and expected matrix of species occupation. The expected matrix was generated using the application of Randomization Algorithms 3 (RA3; sensu Winemiller and Pianka 1990), considering 1000 Monte Carlo simulations, using the software EcoSim (Gotelli and Entsminger 2009).

In order to test the hypothesis whether environmental heterogeneity of breeding ponds influences on species composition, the breeding ponds were characterized according to the five environmental descriptors, and a dissimilarity matrix of breeding ponds (Euclidian Distance; Krebs 1999) was created for each environmental descriptor. The differentiation of species compositions among breeding ponds (beta diversity) was determined by the Jaccard coefficient (C_J; Krebs 1999), and the beta diversity between pairs of compared breeding ponds in the resultant similarity matrix was considered high when $C_J \leq 0.50$. A Mantel test matrix correlation (Manly 1994) was applied to verify if geographical distance among breeding ponds influences on the species composition of breeding ponds. Owing to the significant effect of the geographical distance ($r = -0.31$, $p = 0.002$), a Partial Mantel test (Smouse et al. 1986) was applied between the dissimilarity matrix of each environmental descriptor and the similarity matrix of species composition of the breeding ponds. The Partial Mantel test compares two matrices (A = species composition matrix and B = dissimilarity matrix of each one of the five environmental descriptors), removing the effect of a third matrix (C = matrix of geographical distance of breeding ponds), using a regression of *C* on *A* and *B*, obtaining two residual matrices, which represents the variation part of *A* and *B* that is not explained by *C* (Smouse et al. 1986). Thus, the two residual matrices can be normally compared. The comparisons were made between matrices of dissimilarity and similarity; thus, a negative value of "*r*" was interpreted as a positive correlation, and a positive value was interpreted as a negative correlation. The analyses were performed using the NTSYSpc 2.10s software (Rohlf 2000).

The influence of environmental heterogeneity of breeding ponds on species richness was assessed by the application of a linear multiple regression (Zar 1999), among the anuran species richness (dependent variable) and the five environmental descriptors (independent variables) of each breeding pond. Before performing the analysis, both species richness and environmental descriptor data were $\log_{10}$-tranformed in order to remove the heterogeneity of variance of the original data (correction of the heteroscedasticity of the data, Zar 1999).

Results

The distribution of the 34 anuran species found in the 38 breeding ponds was significantly different from the random occupation of the breeding ponds (mean of expected indices = 0.292 ± 0.000; observed mean overlap = 0.336; $p = 0.000$), and beta diversity was high with 82.36% of combination pairs of breeding ponds had $C_J \leq 0.50$. The main environmental descriptors that determined this variation of species composition among the breeding ponds were the number of edge types ($r = -0.39$, $p = 0.001$), number of plant types along the edges of the breeding ponds ($r = -0.26$, $p = 0.001$), and the hydroperiod ($r = -0.20$, $p = 0.001$). Neither the percentage of vegetation cover on the water's surface ($r = -0.05$, $p > 0.05$) nor the size of the breeding ponds ($r = -0.00$, $p > 0.05$) were correlated with species composition.

The environmental heterogeneity influenced species richness of the breeding ponds ($F_{(5,32)} = 5.95$, adjusted $r^2 = 0.401$, $p = 0.0005$), but the partial regression results indicated that only one environmental descriptor was significant, i.e., the number of edge types (β coefficient = 0.67, $p = 0.000$). No partial regression was found for the four remaining environmental descriptors (Table 3).

Discussion

The distribution of anurans in the 38 breeding ponds was clearly not random, and the hypothesis of environmental influence on species composition was corroborated by the positive correlation of species composition with the number of edge types, the number of plant types along the edges of the breeding ponds, and the hydroperiod. Previous studies of some anuran assemblages that were considered here deviate from the belief in the influence of environmental heterogeneity of breeding ponds on the species composition. One study showed no influence of environmental heterogeneity on species composition (10 breeding ponds of Nova Itapirema; Vasconcelos and Rossa-Feres 2005). Another study showed a correlation between species composition and hydroperiod (eight breeding ponds of Santa Fé do Sul; Santos et al. 2007). A third study showed a correlation between species composition and four environmental descriptors (hydroperiod, depth, vegetation structure, and percentage of vegetation cover; 12 breeding ponds of Icém; Candeira 2007). This inconsistency in results can be related to the number of breeding ponds analyzed in each study, because a major statistical significance tends to be found with a higher number of breeding ponds (present study). Santos et al. (2007) noted that the absence of correlation among the majority of the environmental descriptors and species composition in Santa Fé do Sul could be due to the high homogeneity of the breeding ponds, as a consequence of agricultural impact in the studied region. Thus, only with a higher number of sampled breeding ponds could significant differences be detected, because the only way to reduce the Type I error in statistical analysis (reject a null hypothesis when it is in fact true) is to increase the sampling number (Zar 1999).

Despite of few studies testing the influence of environmental variables on anuran species composition, the importance of environmental heterogeneity is often noted as one of the main factors determining the species composition in a given locality (Parris and McCarthy 1999; Parris 2004; Afonso and Eterovick 2007; Bastazini et al. 2007). Among the environmental descriptors analyzed herein, both the size of breeding ponds and the hydroperiod have been commonly related to species composition in several localities (Afonso and Eterovick 2007; Parris 2004; Santos et al. 2007; Keller et al. 2009). Size was not correlated with species composition in the present study, because the largest breeding ponds sheltered lower species richness than medium-sized ponds. The largest breeding ponds also sheltered fish species that feed on tadpoles (e.g., *Hoplias malabaricus* – Herythrinidae, and the non-native species *Tilapia rendalli* - Cichlidae), which may have decreased amphibian species richness in these ponds (Scheffer et al. 2006). On the other hand, size was considered to be a preponderant factor in determining species composition in streams of Santuário do Caraça, Brazil (Afonso and Eterovick 2007), in Queensland, Australia (Parris and McCarthy 1999), and in Ulu Temburong National Park, Borneo (Keller et al. 2009), where streams of similar size in that region had similar frog assemblages (Parris and McCarthy 1999; Keller et al. 2009). Analyzing a higher number of sampled regions in Australia (Queensland and New South Wales), Parris (2004) also found that stream size influences species composition. This author highlighted the fact that the smallest streams have a shorter hydroperiod, and indicated a possible relationship between the species composition (based on the effects of the adaptive characteristics of each species on the time necessary for tadpole development) and the hydroperiod of the ponds. In the present study, the influence of the hydroperiod on species composition is possibly related to the type of reproductive pattern exhibited by the species, because the permanent breeding ponds, where *k* selection is frequent (i.e., biotic interactions have greater importance on the structure of communities, density-dependent effects are maximal, and the environment is saturated with organisms: sensu Pianka 1970), tend to shelter species that have prolonged reproductive pattern throughout the year (sensu Wells 1977; e.g., *Hypsiboas albopunctatus*). On the other hand, temporary breeding ponds, where the *r* selection is frequent (i.e., climatic factors have a greater influence on the structure of communities, density-dependent process are absent, and competition among species is weak or absent: sensu Pianka 1970), favor the presence of another species group, which has an explosive reproductive pattern (sensu Wells 1977; e.g., *Rhinella schneideri* and *Leptodactylus chaquensis*) (for the temporal distribution of some studied species see Vasconcelos and Rossa-Feres 2005 and Santos et al. 2007).

Vegetation structure has also been considered an important factor affecting species composition, both on regional (Parris 2004; Bastazini et al. 2007) and local (Parris and McCarthy 1999; Afonso and Eterovick 2007; Candeira 2007; present study) scales. Vegetation complexity is represented on a regional scale as a type of forest formation, which can shelter different frog fauna, from dry and shrubby forest to moist forest with higher stratification (Parris 2004; Bastazini et al. 2007). A higher number of specializations on reproductive modes is found in areas with higher moisture and vegetation heterogeneity, as a consequence of the large number of humid microhabitats available for anurans (Haddad and Prado 2005). On a local scale, vegetation heterogeneity is important for anurans because it provides higher humidity, more shelters, and more vocalization and oviposition sites (Parris and McCarthy 1999; Afonso and Eterovick 2007; Candeira 2007). In the current study, vegetation heterogeneity is probably most important for providing vocalization sites for treefrog species (Hylidae), because the partitioning of calling sites tends to be found among Hylidae species, which utilize the three-dimensional space of the environment (Santos and Rossa-Feres 2007; Vasconcelos and Rossa-Feres 2008).

The variable number of edge types (gradient of humidity and vegetation in the margins) influenced both the richness and composition of the species, because breeding ponds with edges composed of drier soils without vegetation sheltered fewer species, most of them considered generalists in the occupation of the breeding ponds in the studied region (e.g., *Scinax fuscovarius* and *Leptodactylus fuscus*; Rossa-Feres and Jim 2001; Vasconcelos and Rossa-Feres 2005; Santos et al. 2007). Low species richness in breeding ponds with dry soil and without vegetation is expected, because there are no microhabitats available for some species that establish their calling sites in wet or swampy soils (e.g., *Leptodactylus podicipinus* and *Pseudopaludicola* aff. *saltica*; Santos and Rossa-Feres 2007; Vasconcelos and Rossa-Feres 2008). In addition, the absence of vegetation can increase the risk of predation of frogs during calling activities, because the escape behavior in closer range of predator approach is more frequent in sites with vegetation (Martín et al. 2005).

Studies assessing the influence of environmental heterogeneity of breeding ponds on anuran species richness are recent and different results are commonly recorded concerning the influence of one specific environmental descriptor. This scenario makes it difficult to establish of a common pattern for anurans. For instance, size of breeding ponds can have a positive correlation (i.e., the larger the breeding pond, the higher the species richness; Parris and McCarthy 1999; Ricklefs and Lovette 1999; Babbitt 2005; Burne and Griffin 2005; Werner et al. 2007), a negative correlation (i.e., the larger the breeding pond, the lower the species richness; Scheffer et al. 2006; Afonso and Eterovick 2007), or it can have no influence on species richness (Oertli et al. 2002; present study). The hydroperiod of breeding ponds has been generally related to species richness (Babbitt 2005; Burne and Griffin 2005; Werner et al. 2007), where temporary breeding ponds with a long duration tend to have higher species richness than permanent and/or temporary breeding ponds with a short duration (Babbitt and Tanner 2000; Weyrauch and Grubb 2004), which is related to the intermediate disturbance hypothesis (Huston 1994) and/or predation pressure (Scheffer et al. 2006). Other environmental characteristics that deserve attention are the negative interference of the canopy cover on species richness of breeding ponds (owing to the lower quantity and quality of resources in these ponds; Burne and Griffin 2005; Werner et al. 2007) and the greater species richness among closer breeding ponds, indicating that pond connectivity (metapopulation dynamics) may play an important role in anuran communities, and may contribute to species turnover among ponds (Burne and Griffin 2005; Vitt and Caldwell 2009).

Parris and McCarthy (1999) concluded that the analysis of the effects of environmental heterogeneity on species richness was not an informative measure for frog assemblages in Queensland (Australia). On the other hand, these authors found a more valuable understanding for conservation management in the analysis of the effects of environmental heterogeneity on species composition. Similarly, three out of five environmental descriptors that were analyzed here were correlated with species composition, while only one descriptor was correlated with species richness. Thus, a high beta diversity (i.e., distinct species composition among breeding ponds) can be found in breeding ponds with similar degrees of species richness. In conclusion, the species composition of anurans from the studied region, rather than species richness, must be the primary consideration for conservation purposes. In terms of management of breeding ponds, different environmental descriptors must be considered in order to shelter a specific anuran assemblage for each type of breeding pond.

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Table 1: Anuran distribution among four studied localities, reproductive modes, and general occurrence of studied species. I = Icém (Candeira 2007), MDSP = Morro do Diabo State Park (Santos et al. 2009), NI = Nova Itapirema (Vasconcelos & Rossa-Feres 2005), SFS = Santa Fé do Sul (Santos et al. 2007). RM = reproductive modes sensu Haddad & Prado 2005, D = species distribution in South America according to Duellman 1999: O = species occurring preferentially in open area (Cerrado-Caatinga-Chaco complex), O/F = species occurring in open area and forest as well (e.g., Amazonian and/or Atlantic Forest); * = occurrence of species in surrounding area (not in the studied breeding ponds).

	I	MDSP	NI	SFS	RM	D
Chiasmocleis albopunctata		■			1	O/F
Dendropsophus elianeae	■		■	■	1	O
Dendropsophus minutus	■	■	■	*	1	O/F
Dendropsophus nanus	■	■	■	■	1	O
Dendropsophus sanborni			■		1	O/F
Dermatonotus muelleri	■			■	1	O
Elachistocleis bicolor		■	■		1	O/F
Elachistocleis spp.	■		■	■	1	O
Eupemphix nattereri	■	■	■	■	11	O
Hypsiboas albopunctatus	■	■	■	■	1,2	O/F
Hypsiboas faber		■			4	O/F
Hypsiboas punctatus		■			1	O/F
Hypsiboas raniceps	■	■	■	■	1	O/F
Leptodactylus chaquensis		■	■	*	11	O
Leptodactylus furnarius	■		*		30	O/F
Leptodactylus fuscus	■	■	■	■	30	O/F
Leptodactylus labyrinthicus	■	■	■	*	13	O/F
Leptodactylus cf. *ocellatus*	■	■	■		11	O/F
Leptodactylus podicipinus	■	■	■	■	13	O/F
Leptodactylus mystaceus		■			30,31	O/F
Leptodactylus mystacinus	■	■	■		30	O/F
Physalaemus centralis	■		■	■	11	O/F
Physalaemus cuvieri	■	■	■	■	11	O/F

Continue

continuation

	I	MDSP	NI	SFS	RM	D
Physalaemus marmoratus	▨		▨	▨	11	O
Pseudopaludicola aff. *saltica* 1	▨		▨	▨	1	O
Pseudopaludicola aff. *saltica* 2	▨				1	O
Pseudopaludicola mystacalis	▨				1	O
Pseudis platensis	▨	▨	▨		1	O/F
Rhinella schneideri	▨	▨	▨	▨	1	O/F
Scinax berthae		▨	▨		1	O
Scinax fuscomarginatus	▨	▨	▨		1	O/F
Scinax fuscovarius	▨	▨	▨	▨	1	O
Scinax similis	▨	▨	▨	▨	1	O/F
Trachycephalus venulosus	▨	▨	▨	▨	1	O/F

Table 2: Categorization of the 38 studied breeding ponds, according to the five environmental descriptors: a) number of edge types (ET): 1) dry soil without vegetation, 2) dry soil with and without vegetation, 3) humid soil without vegetation, 4) humid soil with and without vegetation, 5) flooded soil without vegetation, 6) flooded soil with and without vegetation; b) hydroperiod of breeding ponds (HYDR): 1) permanent, 2) semi-permanent (reduction of water volume over than 90% of the breeding pond), 3) long temporary (duration between six and eleven months), and 4) short temporary (less than six months); c) plant types (PT) in the edge: 1) presence of only creeping herbaceous vegetation, 2) presence of creeping and erect herbaceous vegetation, 3) presence of creeping and erect herbaceous vegetation and shrubby vegetation, 4) presence of creeping and erect herbaceous vegetation, shrubby, and arboreal vegetation; d) size of breeding ponds (SIZ): 1) up to 70m^2, 2) between 71 and 319m^2, 3) between 320 and 800m^2, and 4) over than 801m^2; e) percentage of vegetal cover in water surface (VC): 1) 0-25%, 2) 26-50%, and 3) 51-75%; 4) 76-100%. PP = Permanent Pond, PS = Permanent Swamp, SPP = Semi-permanent Pond, S = Swamp, TP = Temporary Pond, TS = Temporary Swamp. Number in parentheses in front of abbreviations of breeding ponds means their respective anuran species richness.

	Geographic coordinates	**ET**	**HYDR**	**PT**	**SIZ**	**VC**
Icém (Candeira 2007)						
TP1 (3)	20º21’96’’S; 49º15’35’’W	3	3	2	3	1
TP2 (15)	20º21’22’’S; 49º12’07’’W	6	3	4	2	4
TP3 (10)	20º21’18’’S; 49º12’14’’W	6	4	2	1	4
TP4 (3)	21º21’24’’S; 49º12’07’’W	2	4	2	2	1
TP5 (7)	20º22’07’’S; 49º12’02’’W	6	3	2	1	2
PP1 (12)	20º21’50’’S; 49º14’18’’W	6	1	3	2	1
PP2 (10)	20º22’30’’S; 49º16’32’’W	6	1	4	3	2
PP3 (17)	20º21’18’’S; 49º12’17’’W	6	1	2	3	1
PP4 (15)	20º21’50’’S; 49º11’38’’W	6	1	3	3	2
S1 (11)	20º21’46’’S; 49º14’11’’W	6	1	4	3	4
S2 (11)	20º21’30’’S; 49º11’55’’W	6	1	3	3	4

cont.

continuation

	Geographic coordinates	**ET**	**HYDR**	**PT**	**SIZ**	**VC**
S3 (10)	20º21’48’’S; 49º11’36’’W	6	1	4	3	4
Nova Itapirema (Vasconcelos and Rossa Feres 2005)						
PP1 (15)	21º04’41’’S; 49º32’20’’W	6	1	4	3	3
PP2 (17)	21º04’33’’S; 49º32’21’’W	6	1	3	2	3
PP3 (18)	21º04’52’’S; 49º31’09’’W	6	1	3	2	2
PP4 (20)	21º04’25’’S; 49º31’08’’W	6	1	3	3	1
TP1 (20)	21º04’40’’S; 49º32’23’’W	6	3	3	3	3
TP2 (19)	21º04’44’’S; 49º32’20’’W	6	3	3	1	1
TS (18)	21º04’24’’S; 49º31’08’’W	6	3	4	1	1
PS (13)	21º04’28’’S; 49º31’14’’W	6	1	3	1	3
Morro do Diabo State Park (Santos et al. 2009)						
PP1 (8)	22º37’01’’S; 52º10’08’’W	6	1	4	4	1
PP2 (11)	22º22’10’’S; 52º19’43’’W	6	1	4	4	1
PP3 (6)	22º37’00’’S; 52º10’09’’W	6	1	4	2	4
PP4 (7)	22º27’03’’S; 52º20’43’’W	4	1	4	4	1
PS (13)	22º37’01’’S; 52º10’08’’W	6	1	4	4	4
SPP (16)	22º32’47’’S; 52º14’02’’W	6	2	4	4	1
TP1 (10)	22º37’02’’S; 52º10’01’’W	6	4	4	2	2
TP2 (9)	22º37’06’’S; 52º10’05’’W	6	4	4	2	4
TP3 (18)	22º37’10’’S; 52º09’55’’W	6	4	4	4	2
TP4 (14)	22º37’07’’S; 52º10’01’’W	6	4	4	3	4
Santa Fé do Sul (Santos et al. 2007)						
S1 (12)	20º11’20’’S; 50º53’47’’W	6	3	3	4	4
S2 (9)	20º11’05’’S; 50º53’40’’W	6	3	3	3	4
TP1 (5)	20º11’08’’S; 50º53’26’’W	6	3	2	1	1
TP2 (7)	20º11’07’’S; 50º53’40’’W	5	3	2	1	1
TP3 (11)	20º10’42’’S; 50º53’32’’W	6	3	2	2	1
PP1 (8)	20º11’07’’S; 50º53’37’’W	6	1	3	2	4
PP2 (5)	20º11’03’’S; 50º53’40’’W	6	1	3	1	3
PP3 (6)	20º11’03’’S; 50º53’40’’W	6	1	3	2	1

Table 3: Beta Coefficient (± standard deviation) and significance level of the test (*p*) of independent variables resulted from the multiple linear regression analysis (dependent variables = species richness of breeding ponds). Significance of the statistical test: $p < 0.05$.

Variables	BETA Coefficient	*P*
Number of plant types in the edge of breeding ponds	0.12 ± 0.16	0.469
Percentage of vegetal cover in water surface	-0.12 ± 0.14	0.391
Number of edge types*	0.67 ± 0.15	0.000
Hydroperiod of breeding ponds	0.15 ± 0.14	0.287
Size of breeding ponds	0.22 ± 0.15	0.158

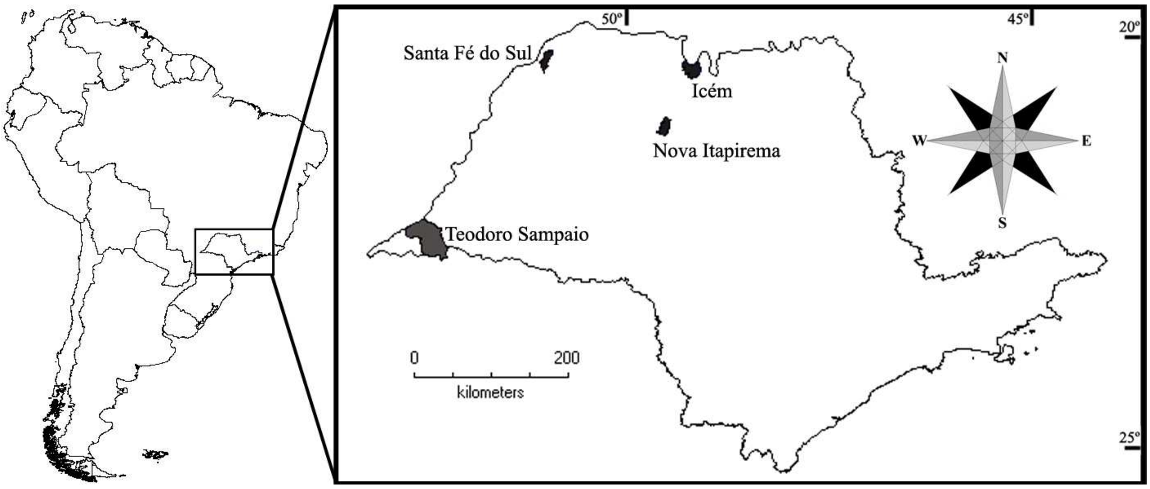

Figure 1**.** Geographic localization of the studied areas: municipality of Icém (20º20'S; 49º11'W), Nova Aliança (district of Nova Itapirema: 21º04'S; 49º32'W), Santa Fé do Sul (20º11'S; 50º53'W) and Teodoro Sampaio (22º32'S; 52º11'W), state of São Paulo. Figure generated by DIVA-GIS software (free online content: Hijmans et al. 2005).

CONCLUSÕES GERAIS

- A anurofauna do PEMD apresentou alta diversidade beta (tanto para ocorrência de machos em atividade de vocalização quanto para ocorrência de girinos), o que significa que existe uma alta substituição de espécies entre os diferentes corpos d’águas selecionados. Isto foi relacionado principalmente com o tipo de correnteza e hidroperíodo dos corpos d’água, sendo que córregos, poças permanentes/semi-permanentes e poças temporárias abrigaram anurofauna diferente entre elas.
- A distribuição temporal das espécies foi restrita aos meses da estação quente e úmida do ano (com exceção para *Rhinella ornata*, que vocalizou e se reproduziu nos meses da estação seca e fria), resultando em sobreposição temporal da atividade de vocalização dos machos e ocorrência dos girinos. Apesar da sobreposição temporal, grupos de espécies apresentaram ocorrência diferenciada durante a estação chuvosa, sendo encontrado espécies típicas de início, meio e fim da estação chuvosa. A ocorrência temporal da riqueza e abundância de girinos foi correlacionada com temperatura e chuva respectivamente.
- A segregação espacial (i.e., ocorrência de espécies de acordo com os diferentes tipo de corpos d’água) e sobreposição temporal das espécies (ocorrência temporal restrita aos meses mais chuvosos do ano para a grande maioria das espécies) nos permite concluir que espaço é a dimensão de nicho mais importante para coexistência das espécies de anuros do PEMD do que a dimensão temporal.
- As principais implicações do presente estudo para conservação são: a proteção de grandes áreas do PEMD, permitindo a proteção de diferentes tipos de corpos d’água (córregos e poças com diferentes hidroperíodos), certificando assim a segurança de espécies

com diferentes padrões de reprodução; manejo dos corpos d'água, incluindo a remoção da espécie do peixe exótico (*Tilapia rendalli* - Cichlidae) em alguns corpos d'água estudados.

- A análise de similaridade evidenciou uma alta diversidade beta entre a anurofauna de cinco diferentes fitofisionomias amostradas no PEMD, o que é conseqüência da baixa eficiência de captura da metodologia empregada (armadilhas de interceptação e queda), o que resultou em uma baixa riqueza de espécies nas fitofisionomias.
- Alta similaridade na composição de espécies só foi registrada entre as fitofisionomias mais preservadas do PEMD, o que foi relacionada com o uso preferencial de hábitat pela espécie *Rhinella ornata*. De fato, a análise de táxons indicadores evidenciou que a área mais preservada do parque é indicada pela presença de *R. ornata*, enquanto que as espécies de leiuperídeos *Eupemphix nattereri* e *Physalaemus cuvieri*, considerados generalistas na ocupação do ambiente, foram indicadores da floresta em estágio avançado de regeneração.
- Dentre os cinco descritores da heterogeneidade ambiental das poças estudadas, apenas três (número de tipos de margem, número de estratificações vegetais presentes nas margens e hidroperíodo das poças) influenciaram na composição de espécies de anuros, enquanto somente um descritor (número de tipos de margens) foi relacionado com a riqueza de espécie de anuros.
- A correlação de três descritores ambientais das poças com a composição de espécies de anuros e somente um descritor correlacionado com a riqueza de espécie sugere que uma estratégia de conservação efetiva deve primeiramente considerar a composição de espécies, pois corpos d'água com um mesmo número de espécies podem abrigar uma diferente composição de espécies.