

## THIAGO AUGUSTO PIRES

# PHYLOGENETIC, TAXONOMICAL, FUNCTIONAL AND DIVERSITY AND THE STRUCTURE OF ANURAN COMMUNITIES IN COASTAL PLAINS OF SÃO PAULO STATE, SOUTHEASTERN BRAZIL

# DIVERSIDADE FILOGENÉTICA, TAXONÔMICA E FUNCIONAL E A ESTRUTURA DE COMUNIDADES DE ANUROS NAS PLANÍCIES COSTEIRAS DO ESTADO DE SÃO PAULO, SUDESTE DO BRASIL

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#### ABSTRACT

Generally, biological communities can be structured by elements that occurring in different spatial scales, which include biotic factors (e.g., competition and predation); abiotic factors (e.g., environmental heterogeneity); historical (e.g., colonization and extinction events); and neutral dynamics (e.g., local and random dispersal and extinctions). One of the most interesting approaches to study the structure of communities is based on the investigation of how different processes and mechanisms influence different scales or components of biodiversity. Such as the beta diversity component, a measure of dissimilarity between communities primarily assessed through the presence and absence of species in each community. Another method used by ecologists to understand the structure of communities is the evaluation of the phylogenetic and functional structure of the community. Through the assessment of these properties and the possible factors that may influencing it, is possible to comprehend the rules for assembly and maintenance of communities. In this context, our general objectives in this dissertation were: estimate the tadpoles' beta diversity from coastal plains of São Paulo states, in its different components: functional, taxonomic and phylogenetic; examine spatial and environmental predictors that best explain the variation in the three evaluated components of the beta diversity; assess the phylogenetic and functional structure of tadpoles' communities; test the traits phylogenetic conservation of tadpoles to better understand the phylogenetic and functional structure; and investigate the environmental predictors that better explain the variance in phylogenetic and functional structure of tadpoles' communities. We found that the spatial predictors explain more variation in the different faces of beta diversity studied here. This result demonstrates the existence of a clear spatial structure in different components of tadpoles' beta diversity

in the coastal plains of the Atlantic Forest in the state of São Paulo. Although much less important, the selected environmental variables (e.g., water conductivity, pH and vegetation structure) also explain an important fraction of the variation in the different components of beta diversity. The variance of taxonomic, functional and phylogenetic tadpoles' beta diversity showed a similar spatial structure as well as environmental structure. This result could be revealing that processes similar (spatial or ecological) may be structuring beta diversity of anuran in the coastal plains. Another interesting result is that out of 33 communities assessed, 18 showed phylogenetic structure (phylogenetic clustering) and 12 displayed an aggregated functional structure. Furthermore, the diversity of tadpoles' traits is significantly concentrated in a few nodes and close to the root of the phylogeny, showing that tadpoles present traits phylogenetic conservation in the study area. A significant part of the variation in the phylogenetic structure of communities is explained by six environmental variables selected, such as presence of potential predators, external vegetation structure diversity and canopy cover, variables also significant to the functional structure, among the five selected. All variables are significant for development and survival of tadpoles. Thus, these results demonstrate the important role of ecological (environmental filters) and evolutionary processes (phylogenetic conservatism of traits) in functional structure, reflected even in phylogenetic structure of anurans in coastal plains.

#### RESUMO

Em termos gerais, comunidades biológicas podem ser estruturadas por elementos que ocorrem em escalas espaciais diversas, que incluem fatores bióticos (e.g., competição e predação); fatores abióticos (e.g., heterogeneidade ambiental), históricos (e.g., eventos de extinção e colonização; e dinâmicas neutras (e.g., dispersões e extinções locais e aleatórias). Uma das formas mais interessantes de se estudar a estrutura de comunidades é a partir da investigação de como diferentes processos e mecanismos influenciam diferentes escalas ou componentes da biodiversidade. Por exemplo, o componente da diversidade beta, uma medida de dissimilaridade entre comunidades, primariamente avaliada através da presença e ausência das espécies em cada comunidade. Outra forma utilizada por ecólogos para compreender a estrutura de comunidades é avaliar a estrutura filogenética das comunidades. Através da avaliação dessas propriedades e quais possíveis fatores a influenciam, se torna possível compreender as regras de montagem e manutenção de comunidades. Nesse contexto, nossos objetivos gerais nessa dissertação foram: estimar a diversidade beta de anuros das planícies costeiras paulistas em seus diferentes componentes: funcional, taxonômico e filogenético; examinar quais preditores espaciais e ambientais melhor explicam a variação nos três componentes da diversidade avaliadas; avaliar a estrutura filogenética e funcional das comunidades de anuros; testar a conservação filogenética de atributos nos girinos para melhor compreensão da estrutura filogenética e funcional; e analisar quais preditores ambientais explicam melhor a variação na estrutura filogenética e funcional dos anuros. Encontramos que os preditores que mais explicam a variação nas diferentes faces da diversidade beta estudadas aqui (i.e. taxonômica, funcional e filogenética) são as variáveis espaciais. Esse resultado demostra a existência de uma clara estrutura espacial nas diferentes faces diversidade beta de anuros nas planícies costeiras da mata atlântica no estado de São Paulo. Embora bem menos importante, as variáveis ambientais selecionadas (e.g. condutividade da água, pH e estrutura vegetal) também explicam uma fração importante da variação dos diferentes componentes da diversidade beta de anuros. As variações da diversidade beta taxonômica, funcional e filogenética dos girinos apresentam uma estrutura semelhante espacial assim como ambiental. Esse resultado pode estar revelando que processos, espaciais ou ecológicos, semelhantes, podem estar estruturando a diversidade beta de anuros nas planícies costeiras. Outro resultado interessante é que encontramos foi que das 33 comunidades avaliadas, 17 apresentam uma clara estrutura filogenética (agrupamento filogenético) e 12 apresentaram uma estrutura funcional agregada. A diversidade de atributos dos girinos é significantemente concentrada em poucos nós e próximos da raiz da filogenia, demostrando que girinos apresentam conservação filogenética de atributos na região estudada. Uma significante parte da variação na estrutura filogenética das comunidades é explicada por seis variáveis ambientais selecionadas, tais como a presença de potenciais predadores, diversidade de vegetação externa, cobertura de dossel, variáveis importantes, dentre as cinco selecionadas, para a estrutura funcional. Todas essas variáveis são importantes para o desenvolvimento, sobrevivência e consequentemente a ocorrência de anuros. Assim, estes resultados demonstram o importante papel dos processos ecológicos (filtros ambientais) e evolutivos (conservação filogenética de atributos) na estrutura funcional, refletida inclusive na estrutura filogenética de anuros em planícies costeiras.

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#### CONSIDERAÇÕES INICIAIS

Uma das questões mais antigas e centrais em ecologia está relacionada a compreensão dos processos que determinam ou estruturam os diferentes padrões de composição, distribuição e abundância de espécies em comunidades ecológicas (Parris 2004; Vellend 2010). Diversas hipóteses têm sido levantadas e testadas desde a primeira metade do século XX, com o objetivo de elucidar essas questões, tanto em menores escalas, por exemplo, em comunidades locais (Hutchinson 1959; Diamond 1975) como, mais recentemente, em escalas mais abrangentes (Ricklefs 1987), por exemplo, em metacomunidades.

Isso porque em termos gerais, comunidades biológicas e mais amplamente, metacomunidades, podem ser estruturadas por elementos que ocorrem em escalas espaciais diversas, que incluem fatores bióticos (e.g., competição, predação e facilitação; Hutchinson 1959; Diamond 1975), fatores abióticos (e.g., heterogeneidade ambiental, clima e pluviosidade; Davies et al. 2007), históricos (e.g., eventos de extinção e colonização; (Tofts & Silvertown 2000; Ackerly 2003) e neutros (extinção local e dispersão aleatória; Hubbell, 2001). Nesse sentido, a metacomunidade é um "framework" multi-escala que busca integrar a dispersão e a heterogeneidade ambiental entre diferentes comunidades para explicar a variação na composição de espécies entre as mesmas (Chase, 2003). Assim, a metacomunidade se define como os conjuntos de comunidades locais conectadas por dispersão de múltiplas espécies, e que possuem potencial de interação entre si, integrando as comunidades em diversas escalas (Leibold et al., 2004; Ricklefs, 2008).

1

Ainda em 1859, Darwin já postulava que a competição será mais severa entre esses indivíduos das mesmas espécies (competição intraespecífica), ou espécies mais próximas (competição interespecífica), pois esses organismos tendem a ser mais ecologicamente similares. Já Gause (1934), discute de forma genérica como competição entre indivíduos são importantes para as comunidades ecológicas. Mais tarde, Hutchinson (1959), Hardin (1960), MacArthur & Levins (1967) discutem como a similaridade de nicho e a competição entre as espécies podem estruturar a diversidade de uma comunidade. Essas discussões culminam no principio de competição exclusiva, que postula que as espécies ecologicamente iguais irão se excluir mutualmente em uma assembleia de espécies, e somente o competidor mais apto irá se manter nessa comunidade (Hardin 1960). E assim, as espécies têm de apresentar alguma diferença de nicho para poderem coexistir na mesma comunidade (MacArthur & Levins (1967).

Já na década de 70, outros autores como Mueller-Dombois & Ellenberg (1974), argumentam que as condições ambientais também são importantes para a montagem de uma comunidade, por exemplo, excluindo espécies que não possuem os requisitos necessários para sobreviver sob determinada condição ambiental apresentada nessa comunidade, processo cunhado de filtragem ambiental. Posteriormente, Brooks (1985) desenvolve uma área da ecologia ainda pouco explorada, a Ecologia Histórica, que busca entender o contexto histórico dos padrões de distribuição geográfica de espécies, por exemplo como fatores passados, tais como o surgimento de barreiras geográficas ou mudanças climáticas, podem ter influenciado nas distribuições das espécies. Seguindo essa linha, Ricklefs (1987), discute amplamente as relativas influências de processos em pequenas escalas (locais) até escalas mais amplas (regionais), principalmente sobre a diversidade de espécies.

Já no inicio da década de 2000, Hubbell (2001), propõem a Teoria Neutra de Biodiversidade e Biogeografia que levanta a hipótese de que processos estocásticos espacialmente estruturados tais como a dispersão aleatória, podem ter um papel fundamental sobre a estruturação da assembleia de variação composicional. Essa hipótese se baseia na premissa que muitas vezes as espécies componentes dessas comunidades podem ser ecologicamente equivalentes e assim seus parâmetros demográficos são completamente estocástico (i.e., "ecological drift") (para mais detalhes, ver Hubbell 2001). Assim, a variação na composição de espécies entre as comunidades pode ser o resultado de dispersão estocástica, porem espacialmente restringida (Tuomisto e Ruokolainen 2006). Também no início da década de 2000, Webb (2001) propõe uma nova linha de pesquisa em ecologia, a Ecologia filogenética. Nessa linha de pesquisa, buscam-se integrar as relações filogenéticas entre as espécies componentes das comunidades estudadas, com o objetivo de investigar os simultaneamente os fatores ecológicos e evolutivos que podem determinar à montagem e variação entre as comunidades estudadas, por exemplo, estudando a estrutura filogenética de comunidades (Webb et al. 2002).

A estrutura filogenética é uma medida derivada da diversidade filogenética e utilizada para estimar se a comunidade é composta por espécies mais próximas ou mais distantes filogeneticamente que o esperado ao acaso (Webb 2000; Webb et al. 2002). A avaliação da estrutura filogenética de comunidades e seus possíveis preditores pode indicar mecanismos e processos que determinam ou influenciam a estrutura da comunidade (Webb 2000; Webb et al. 2002; Cavender-Bares et al. 2006; Willis et al. 2009). Por exemplo,

quando os atributos fenotípicos são conservados filogeneticamente e existe uma estrutura de agrupamento filogenético (quando as espécies são mais próximas filogeneticamente do que esperado ao acaso) acredita-se que a filtragem ambiental seja o principal processo estruturador (Webb et al. 2002; Cavender-Bares et al. 2009). Porém, a competição também pode resultar em agrupamento filogenético, mesmo quando as espécies possuem conservação filogenética de seus atributos, nesse caso, um clado composto de competidores mais aptos e similares ecologicamente irá se manter na comunidade (Mayfield & Levine 2010). Assim, essas hipóteses necessitam ser de fato testadas, já existem diversos exemplos na natureza, em estudos em ecologia filogenética, que não corroboram essas hipóteses determinísticas (Mayfield & Levine 2010).

Além disso, uma das formas mais interessantes de se estudar a variação estrutural entre comunidades, dentro de uma metacomunidade, é a partir da investigação de como diferentes processos e mecanismos influenciam diferentes escalas ou componentes da biodiversidade. Entre esses componentes da biodiversidade, podemos destacar três formas importantes de medi-la: a tradicional diversidade de espécies ou diversidade taxonômica, a diversidade filogenética e a diversidade funcional (De Bello et al. 2010). Além disso, as comunidades normalmente apresentam uma variação em sua diversidade que é espacialmente estruturada, ou seja, cada componente da diversidade pode apresentar uma variação espacial (De Bello et al. 2010; Dray et al. 2012). Whittaker (1960), estudando a diversidade de arvores dentro de gradientes ambientais, sugeriu o termo diversidade beta para designar a variação espacial ou a mudança de composição dessa composição entre comunidades. Entender a diversidade beta entre comunidades e os fatores que a influenciam tem sido alvo primário para diversos ecólogos (Anderson et al. 2011). E grande

parte desse interesse se deve ao fato de que é possível testar hipóteses especificas sobre os processos e mecanismos que originam a beta diversidade dentro das metacomunidades encontradas na natureza (Legendre & De Cáceres 2013).

De forma geral, a diversidade beta é primariamente avaliada através da presença e ausência das espécies de interesse em uma comunidade (Legendre & De Cáceres 2013). Dentro deste contexto, é interessante destacar que a presença de uma ou de um conjunto de espécies em um dado local, depende geralmente de fatores que podem atuar sinergicamente e assim influenciar o processo da montagem das comunidades ecológicas e assim a biodiversidade local, como a filtragem ambiental (Lebrija-Trejos et al. 2010), competição (Macarthur & Levins 1967; Diamond 1975) e/ou dispersão de espécies (Hubbell 2001; Fig. 1).

Além disso, a montagem de uma dada comunidade local depende, até certo nível, do conjunto de espécies disponível para colonizar e se manter nessa comunidade, e a esse conjunto se dá o nome de pool regional de espécies (Ricklefs 1987; Chase 2003). A existência desse conjunto de espécies depende de fenômenos ou eventos que ocorrem em escalas espaciais e temporais maiores do que a observada em comunidades locais, como processos biogeográficos, incluindo a dispersão e migração, processos neutros como dispersão aleatória, e processos evolutivos, como especiação e extinção (Ricklefs 1987; Hubbell 2001; Wiens & Donoghue 2004; Willis et al. 2009; Fig. 1). Desse pool regional de espécies, são montadas ou estruturadas as comunidades locais e a manutenção de cada espécie na comunidade será mediada por processos demográficos locais e por sua aptidão para tolerar as interações bióticas (e.g. competição, predação) e interações com fatores abióticos (Vellend 2010; Fig. 1).

5



Figura 1. Diagrama esquemático dos processos relacionados à distribuição de espécies e estruturação de comunidades em diferentes escalas espaciais e temporais. Modificado de Cavender-Bares et al. (2009).

Além disso, as espécies podem compartilhar não somente o habitat que vivem, mas uma história evolutiva comum. Isso porque a interação entre as espécies é mediada pelas diferenças fenotípicas e comportamentais entre elas, e essa variação tem, geralmente, base evolutiva, isto é, essas diferenças são provavelmente modificações a partir de um ancestral comum que, em ultima estância, todas as espécies compartilham (Seehausen 2004, Webb et al. 2002). A história evolutiva de grupo taxonômico é determinada pelo grau de parentesco evolutivo compartilhado entre as espécies que pertencem a esse grupo (Harvey & Pagel 1991). Assim, incluindo a história evolutiva compartilhada de um grupo no estudo ecológico, podemos compreender quais possíveis fatores evolutivos estão relacionados com a origem e evolução desse grupo de organismos e como isso pode influenciar a montagem da comunidade (Webb et al. 2002). Portanto, incluir as relações evolutivas entre as espécies no estudo de padrões de diversidade possibilita uma melhor compreensão sobre os processos geradores e mantenedores da própria diversidade. Para esse propósito, nas últimas duas décadas, uma grande parte dos ecólogos tem discutido e incluído a historia evolutiva, a partir de hipóteses filogenéticas, tanto no estudo da estrutura de comunidades, quanto no estudo da variação entre comunidade, por exemplo, analisando a diversidade beta filogenética entre comunidades (Graham & Fine 2008; Swenson 2011; Legendre & De Cáceres 2013).

A diversidade beta filogenética leva em consideração a variação espacial composicional, integrando a história evolutiva entre as espécies, ampliando assim a compreensão sobre a estrutura de comunidades e integrando aspectos ecológicos e evolutivos do processo de montagem da comunidade (Graham & Fine 2008; De Bello et al. 2010). Outra medida importante é o componente funcional da diversidade que também integra atributos fenotípicos aos estudos de diversidade beta e estrutura de comunidades. A diversidade beta funcional leva em consideração a variação espacial nos atributos fenotípicos entre as comunidades. Assim, somos capazes dar mais um passo na compreensão dos processos responsáveis pela montagem e estruturação de comunidades (de Bello et al 2010). Já a estrutura funcional de uma comunidade, assim como a estrutura

filogenética, é uma medida derivada da diversidade funcional (Petchey and Gaston 2002, 2006). Essa medida nos permite saber se os organismos dessa comunidade são mais próximos ou distantes funcionalmente do que esperado ao acaso e assim nos permitindo levantar hipóteses mais robustas sobre os prováveis processos responsáveis por tais padrões. Isso porque os atributos fenotípicos são os mediadores entre as interações bióticas e abióticas das espécies, possuindo então uma forte base ecológica (Pausas & Verdú 2010).

Porem, esses atributos também possuem base evolutiva, e assim podem ser conservados ou convergentes ao longo da história evolutiva das espécies, podendo ser o resultado de processos evolutivos e ecológicos ocorridos no passado (Losos 2008; Emerson & Gillespie 2008). Um passo importante pra compreendermos a evolução desses atributos é medir o sinal filogenético, que irá indicar se determinado atributo é conservado ou convergente entre as linhagens filogenéticas de determinado grupo (Pavoine & Aguette 2010). Assim, a incorporação das informações filogenéticas e de atributos fenotípicos permite avaliar simultaneamente os aspectos ecológicos e evolutivos envolvidos na estruturação e variação espacial entre comunidades (De Bello et al. 2010; Mouquet et al. 2012).

Nas regiões neotropicais, as comunidades ecológicas exibem enorme diversidade biológica (Fischer 1960; Gentry 1982; Albert & Crampton 2005; Funk, Caminer & Ron 2012). Porém, devido à complexidade de se estudar as comunidades ecológicas compostas por todas suas espécies, os ecólogos muitas vezes escolhem algum grupo taxonômico de interesse (Magurran 2004). Dentro de tal biodiversidade, especificamente os anfíbios anuros neotropicais são um excelente grupo animal para investigar os papéis de processos ecológicos, evolutivos e espaciais sobre a estrutura de comunidades. Isso porque, além de apresentar grande número de espécies (946 espécies no Brasil, Segalla et al., 2014), este é um grupo que pode apresentar desde espécies com distribuição ampla até espécies endêmicas (IUCN 2014; Jenkins, Pimm & Joppa 2013). Essa variação de distribuição muitas vezes é indicada como uma resposta a mecanismos ecológicos, espaciais e evolutivos em que tais espécies são extremamente suscetíveis, devido, por exemplo, à sua variabilidade fenotípica, comportamental, ciclo de vida complexo e pele permeável (Haddad & Prado 2005; Keller et al. 2009; Silva et al. 2012; Valdujo, Carnaval & Graham 2013).

Dentro desse contexto teórico, nossos objetivos gerais nessa dissertação são: (1) estimar a diversidade beta de anuros das planícies costeiras paulistas em seus diferentes componentes: diversidade funcional, taxonômica e filogenética; (2) examinar quais preditores espaciais e ambientais melhor explicam a variação nas três faces da diversidade avaliadas; (3) avaliar a estrutura filogenética e funcional das comunidades de anuros; (4) testar a premissa de conservação filogenética de atributos nos girinos para melhor compreensão da estrutura filogenética de comunidades de anuros; e (5) analisar quais preditores ambientais explicam melhor a variação na estrutura filogenética e funcional dos anuros nas planícies costeiras paulistas.

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# DRIVERS OF FUNCTIONAL AND PHYLOGENETIC STRUCTURE OF ANURANS ALONG THE COASTAL PLAINS, SOUTHEASTERN BRAZIL

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## ABSTRACT

How ecological, historical and evolutionary factors affect the structure of ecological communities? In order to answer this question, one can assess the phylogenetic and functional structure of a community and discuss which factors might be influencing it. Herein, we aim to evaluate the phylogenetic and functional structure of 33 amphibian anuran tadpole communities in coastal plains of the Atlantic forest in Southeastern Brazil, and assess the relative importance of environmental variables potentially related to the phylogenetic and functional structure of these communities. We also tested the assumption of phylogenetic conservatism of tadpoles' traits of these communities, to properly interpret the phylogenetic structure. We found that 32 communities showed positive values of phylogenetic structure, 18 of them being significantly clustered. A aggregated functional structure was found in 12 of the 33 communities analyzed. The trait diversity of tadpoles was skewed to the root, so we concluded that tadpoles' communities show phylogenetic trait conservatism. This could indicate the evolutionary factors as important drivers of community structure. Only six environmental variables were selected as the best explanatory model to the phylogenetic structure, out of 11 evaluated here. The water conductivity, external and internal vegetation structure diversity, canopy cover, and oxygen dissolved were negatively related with the phylogenetic clustering, whereas the presence of potential predators (fishes) was positively related. The best explanatory model to the functional structure included five environmental variables: external vegetation diversity, canopy cover, area, dissolved oxygen and presence of potential fish predator (the only positively related, similarly to phylogenetic structure). All variables represent factors affecting anuran communities, influencing its performance, survivorship, and distribution

and were very similar to phylogenetic and functional structure. In worth to note that, out of the 12 functional structured communities, 10 were phylogenetically structured as well. Thus, our results demonstrate that these factors may be acting as environmental filters, affecting species' traits and even linages occurrence in aquatic communities. Our study provided a better comprehension of the phylogenetic and functional structure in vertebrates, as a result of ecological and evolutionary factors interacting and shaping the anuran assemblages of coastal plains in the Atlantic Forest from Southeastern Brazil.

Keywords: Ecophylogenetics, Community Ecology, Biodiversity, Phylogeny, Functional Traits, Tadpoles, Environmental control, Atlantic Forest

## INTRODUCTION

A crucial demand to ecologists is to determine and distinguish how the contemporary and historical factors interact and affect the species assembly, and then the overall communities' structure (Ricklefs 1987, Ricklefs and Schluter 1993, Webb et al. 2002, 2008). Lately, there has been an expressive attention on the significance of evolutionary factors in the structure of ecological communities and the potential of phylogenetic data to increase our understanding on such processes (Webb et al. 2002, 2008, Johnson and Stinchcombe 2007, Cavender-Bares et al. 2009). Also recently, a challenge of community ecology raised, the aim to comprehend the processes driving the functional structure of ecological communities, for instance, niched-based processes (Mouillot et al. 2011, Villeger et al. 2010). Thus, Studies on structure of ecological communities based on a phylogenetic and functional perspective correspond to an appropriate approach to investigate these phenomena because this approach are complementary. This is because the assessment of phylogenetic structure of ecological communities gives us insights about the evolutionary and ecological mechanisms and processes which can determine or influence the community structure (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2004, 2006, Graham et al. 2009, Willis et al. 2010). While the functional structure of communities could reveals in a more detailed and reliable way, about the possible ecological mechanisms driving the structure of the community, as this structure may the outcome of the interact of the functional traits of regional pool of species and habitat parameters displayed in each potential community (Mouchet et al. 2010, Mouillot et al. 2011, Villeger et al. 2010)

In this perspective, one way to assess the phylogenetic structure of ecological communities is to quantify the phylogenetic distance between species occurring in a given

assemblage and to compare the observed distances to a null expectation. This framework make possible to determine the phylogenetic structure of an assemblage. The MPD is a standardized metric of the mean pairwise phylogenetic distance of taxa in a sample, which quantifies the phylogenetic clustering (positive values) or overdispersion (negative values) of taxa in a particular community, comparing theses value to a null model (Webb et al. 2002; Cavender-Bares et al. 2009). This metric has been used in several studies and it would be the first step to investigate the ecological and evolutionary mechanisms driving phylogenetic structure of communities (e.g. Webb 2000, Graham et al. 2009, Letcher 2010, Cardillo 2011, Swenson et al. 2012).

In this ecophylogenetic framework, a relatively well accepted ecological hypothesis suggests that, environmental drivers act as 'filters' constraining the assemblage of communities, i.e. progressively selecting species best adapted to local conditions from the regional pool, when the species' traits associated with this drivers is phylogenetically conserved (Webb, 2001). However, interspecific competition could be the main mechanism to a clustering pattern, when for instance closely related species have ecological differences which confer competitive ability in relation to other species of the community. Thus, to correctly investigate the drivers that may be determinant to ecological structure of a community, we should not just infer the processes of patterns of phylogenetic structure of communities, but in fact evaluate the relationship between the species biology with environment.

For instance, amphibians, and particularly anurans, are affected by environmental variables such as canopy cover, argued as indirectly affecting the performance and the occurrence of anurans in ponds (Skelly et al. 2002, Werner et al. 2007). As well as

vegetation heterogeneity, a vital resource to anurans' reproduction in ponds (Gascon 1991, Moreira et al. 2010, Wassens et al. 2010, Silva et al. 2011, 2012a, da Silva et al. 2012b). And physic-chemistry parameters of water, including pH or oxygen dissolved, which is understood to influence directly and indirectly several aspects of anuran biology, for instance, the development, survival so the occurrence of anurans in ponds (Leuven et al. 1986, Warner et al. 1991, 1993, Pehek 1995, Moore & Townsend Jr 1998, Alford 1999, Ultsch et al. 1999).

In this perspective, this notorious relationship between environmental biology of amphibians is commonly mediated by ecomorphological traits, which are the outcome of ecological and evolutionary processes (Emerson and Gillespie 2008, Losos 2008). An interesting and innovative approach of asses the association between functional traits and the environment, is investigating the functional structure of the community and what factors can influence it. This can achieve, measuring the mean functional distance (MFD) between communities, derived from the Functional Diversity (FD, Petchey and Gaston 2002, Petchey and Gaston 2006). Thus, positive values indicate community has species that are more functionally different; therefore, this community is expected to shows a high degree of niche partitioning between species. On the other hand, negative values of MFD indicate niche overlap, because the species in these communities are likely to be more functionally similar to each other.

However, in order to improve understand and interpret properly the phylogenetic and functional structure of communities (i.e. MPD and MFD, respectively) and the factors that may be affecting, the relationship of phylogenetic relatedness and ecological traits of species (i.e., Phylogenetic Niche Conservatism - PNC), should be tested (Losos 2008). This can be accomplished by testing the tendency for closely related species to be more phenotypically similar each other (i.e. phylogenetic signal), when compared with species that are drawn randomly from the phylogenetic tree, and quantifying the phylogenetic signal of the organisms of interest (Blomberg and Garland Jr 2002, Losos 2008, Pavoine et al. 2010, Wiens et al. 2012). In other words, it allow us understand if PNC is the outcome of other factors causing closely related species to be more ecologically similar than it would be expected exclusively under Brownian motion evolution (Blomberg and Garland Jr 2002, Losos 2008).

Although there has been an impressive increase in the availability of phylogenetic hypothesis in the last decades and a relevant development in the statistical approaches to phylogenetic studies of ecological communities, it has not been appropriately reached to the most group of taxa (Webb et al. 2002, Vamosi et al. 2009, Cavender-Bares et al. 2009). The anuran amphibians are one of the vertebrate groups most diversified of the Neotropical region (Jenkins et al. 2013), particularly in the Brazil (942 species, Segalla et al. 2014), with several phylogenetic hypothesis available (Faivovich et al. 2005, Frost et al. 2006, Grant et al. 2006, Pyron and Wiens 2011). However, only recently this group has received attention from an ecophylogenetic perspective (e.g., Rosauer et al. 2009, Wiens et al. 2011, Silva et al. 2012b). Anurans are an interesting model to investigate the mechanisms related to the phylogenetic structure of communities. Owing to their complex life cycle, permeable skin, limited dispersal and other ecophysiological and ecomorphological characteristics, anurans are highly sensitive to ecological and evolutionary processes, such as environmental control and speciation (Kozak and Wiens 2006, Becker et al. 2007, Keller et al. 2009, Silva et al. 2011, Silva et al. 2012a, b).

In this study, we aim to evaluate the phylogenetic and functional structure of anuran tadpole assemblages in coast plains of Atlantic Forest in Southeastern, Brazil. We also tested the assumption of phylogenetic conservatism, using a "tips/root skewness" test, as suggested by Pavoine and Aguette (2010), in order to interpret properly the phylogenetic and functional structure, and also assess the relative importance of different environmental drivers of the phylogenetic and functional structure of tadpoles' communities. Based on the arguments presented here and especially in the strong association of a anurans' biology with environmental conditions, we discuss the hypothesis of the environmental control in anuran's communities, by testing the following predictions: (1) the anuran tadpole communities will show a clustered phylogenetic and functional structure; because (2) the tadpoles will exhibit traits phylogenetically conserved; and (3) the variance of phylogenetic and functional structure of ponds will be strong related to environmental factors, such as vegetation structure and physic-chemical parameter of ponds.

### MATERIAL AND METHODS

### STUDY AREA

This study area includes most of the coastal plains of the state of São Paulo. This region has approximately 550 km of extension and have a particular geomorphological history (Suguio and Martin 1978). The coastal plains of this region are bounded on southern and northern by Precambrian basements of the Serra do Mar complex (Suguio and Martin 1978). Moreover, the coastal plains within this region are limited by narrow headlands of Precambrian rocks (Suguio and Martin 1978).

The climate of the study region is of the type Af, following the Köppen climate classification (Peel et al. 2007), with mean annual precipitation ranging between 1800 and 2000 mm, mean minimum temperature of 19°C, and mean maximum temperature of 27°C (Melo and Mantovani 1994). This region is located within the Atlantic Forest domain (Ab'Saber 1977), and is composed by herbaceous, shrubs and forest formations, classified as "restinga" forests and ombrophilous lowland forests (Marques et al. 2011). These formations are heterogeneous, varying in height, hydric saturation of the soil, and distance from the Serra do Mar slopes. This heterogeneity depends on the extent of the coastal plains and the characteristics of sandy soils. Moreover, it suffers the influence of distinct sediments, which arise from the adjacent scarps and streams (Klein 1961, Henriques et al. 1986, Mantovani 2000).

## **BIOLOGICAL SURVEYS**

We sampled tadpoles and potential predator (fishes) from 33 ponds in the coastal plains of São Paulo state (Fig. 1). The tadpoles and the potential predators were sampled through swept with dipnet (30 cm of diameter and 3 mm<sup>2</sup> of mesh) in all suitable microhabitats of tadpoles. The tadpoles were determined to species in the laboratory. Specimens were housed at the Coleção Científica de Anfíbios e Répteis do Departamento de Zoologia e Botânica da UNESP, São José do Rio Preto. Each pond were swept during one hour per pond, and sampled three times between October 2011 and April 2012, totaling a sampling effort of 99 hours-person in all ponds.

# ENVIRONMENTAL DATA - sampling and processing

The follow environmental variables were collected in all sampled ponds in order to assess the influence of environmental drivers to the tadpole phylogenetic community structure: area, hydroperiod, water depth, the internal and external vegetation structure diversity, presence of potential fish predators, canopy cover, pH, water temperature, water conductivity and oxygen dissolved level (for details, see Table 1). The canopy cover proportion was measured using Spherical Crown Densiometers. The pH and water conductivity was measured using Extech® ExStik pH Pen. The water temperature and dissolved oxygen was measured using an YSI DO 200 Oxygen Meter. The categorical variable, hydroperiod were coded as dummy variables (Bocard et al. 2011). For numerical variables (water depth, area, water temperature, water conductivity and dissolved oxygen), we extracted the natural logarithm, and standardized by their ranges, subtracting the maximum value by the minimum value of each variable, as suggest in Pavoine et al. (2009), so all numerical variables have the same weight in the analysis.

# PHYLOGENETIC DATA - sampling and processing

To assess the phylogenetic structure of communities through Mean Pairwise Phylogenetic Distance (MPD) and to test the phylogenetic signal for anuran tadpoles, we used the phylogenetic hypothesis proposed by Pyron and Wiens (2011). We constructed a tree based on this phylogenetic hypothesis, including only our regional pool of species. We assigned age estimates for all nodes based on Wiens et al. (2011). We added species absent in the original phylogeny of Pyron and Wiens (2011), using the functions in phytools R package (Revell 2012). We estimated tree branch lengths through the BLADJ algorithm of the Phylocom 4.1 software (Webb et al. 2008). This algorithm was used to evenly interpolate ages of dated nodes to non-dated nodes. The phylogenetic tree for the regional pool was computed using phylomatic tool in Phylocom 4.1 software (Webb et al. 2008), which pruned the tree in order to include species from the regional pool studied here (Fig. 2). The regional pool was composed by all species recorded in the Serra do Mar costal forest (see Rossa-Feres et al. 2011).

# TRAIT DATA - sampling and processing

To test the premise of traits phylogenetic conservatism and calculate mean pairwise functional distance (MFD), we measured phenotypic traits from two to five individuals of each species collected, depending of the number of specimens available for each species. We have taken the follow quantitative morphological measures from tadpoles, in order to obtain ecomorphological traits: body width (BW), musculature caudal width (MCW), height of caudal musculature (HCM), height of dorsal fin (HDF), height of ventral fin (HVF), body length (BL), body height (BH), spiracle's height (SH), and body total length (BTL). We then calculated five ecomorphological traits which potentially represent the habitat use of Neotropical tadpole species (McDiarmid and Altig 1999), based on means of the following index: caudal relative height (CRH = (HCM + HDF + HVF)/BH); body compression (BC = BH/BCM), relative width of caudal musculature (RWCM = HC/CL), relative caudal length (RCL = BL/BTL), and relative spiracle's position (RSP=SH/BH).We also included the follow categorical measures: oral opening (OR), number of denticle rows (NDR), flagellum presence (FP), spiracle's position (SP), eye's position (EP), and body shape (BS). The selection of traits was based on the strong association between them with ecological and biological features such as habitat use, their foraging behaviors that can influence the ecosystem structure and specific defense against predation (Semlitsch 1990, McDiarmid and Altig 1999, Wassersug 2000, Van Buskirk 2002, Strauß et al. 2010, Both et al. 2011). Finally, all index and measures were used to construct a pairwise distance matrix of species' traits, based on the "Gower" dissimilarity for mixed variables (FDM) (Legendre & Legendre, 2012, see Fig. 3 for details of traits).

# DATA ANALYSIS

# Phylogenetic signal

To assess the PNC assumption, we used the "tips/root skewness test" (Pavoine et al. 2010). This metric is an appropriate approach to assess the distribution of the trait diversity across the phylogenetic tree. Furthermore, this test is compatible with the trait global distance among species, proposed by (Pavoine et al. 2009), which handles both categorical and quantitative traits. This test estimates whether the trait diversity is skewed to root, so that the species closely related have more similar trait values (e.g., due to phylogenetic conservatism) or trait diversity is skewed to tips, so that species closely related have highly dissimilar trait values (e.g., due to convergent trait evolution).

This metric is composed of three steps. Firstly, we test if the concentration of trait diversity is on a single node or the "single-node skewness test". In the second step, we test if the trait diversity values are evenly distributed across nodes, and it is called as "few-

nodes skewness test" which complements the "single-node skewness test" to assess whether only a few nodes have higher contributions to trait diversity. Thirdly, we test if the trait diversity is either concentrated near to the root or to the tips, through of the "tips/root skewness test", which assess whether trait diversity is skewed toward the tips of tree or concentrated toward to the root. For this purpose the null hypothesis, in this test, states that observed trait values are randomly distributed through the tips of phylogeny, permuting the tips 999 times, and then compare the permuted values with observed trait diversity values (Pavoine et al. 2010). Subsequently, we calculated the diversity of traits based on the Rao quadratic entropy (Rao 1982, Pavoine et al. 2010)

#### Phylogenetic and functional structure analysis

In order to evaluate the phylogenetic structure of tadpoles, we used MPD. The MDP is standardized measure of the Mean pairwise Phylogenetic Distance of species in a given community, based on Phylogenetic Diversity (PD), developed by Webb et al. (2000) and which has his roots on Faith's PD (Faith, 1992). The PD is the sum of branch lengths of the phylogenetic tree connecting all species within a community. Thus, The MPD<sub>obs</sub> values of each community were compared to 999 permutations of the community matrix (MPD <sub>null</sub>) that was randomized from the regional pool with equal probability (Kembel 2009). Thus, this metrics test whether the communities are assembled by species which are more (i.e., clustering) or less (i.e., overdispersion) phylogenetically related than expected from chance, generating the MPD. The MFD for each pond sampled were calculated using the functions of picante R package (Kembel et al. 2010). Thus, we used for the following analysis only communities with MPD values significantly different than expected by chance.

Additionally, to assess the functional structure of tadpoles, we calculated the Mean pairwise Functional Distance (MFD) as an adaptation of the MPD (Swenson 2014). As in the MPD, we calculate the standardized size effect, but using the functional diversity (FD) to generate the MFD and so its standardized size effect values (Swenson 2014). The FD was calculated based on sum of branch lengths of the functional dendrogram necessary to connect all the species present in a local community. To generate this functional dendrogram, firstly we calculate a distance matrix based on the functional traits. Then, as we had qualitative and quantitative traits, we used a generalization of Gower distance (Legendre and Legendre 2012) dedicated to the treatment of mixed data and then the UPGMA hierarchical clustering, to create the functional dendrogram (Murtagh 1985). The following steps are equivalent to MPD exposed above, comparing the values of MFD<sub>obs</sub> to 999 permutations of the community matrix (MFD <sub>null</sub>) that was randomized from the regional pool with equal probability (Kembel 2009). Also, this metric can test whether the species of community are more or less, in this case functionally, similar than expected from chance, creating the MFD. We used the functions of FD package to generate the tadpoles' functional diversity and the functions of picante R package to calculate the MFD (Swenson 2014, Kembel et al. 2010, Laliberté and Legendre 2010). Thus, we used for the following analysis only communities with MFD values significantly different than expected by chance.

Spatial dependence between samples is commonly observed in nature, and it can cause noise and bias to the statistical modeling if not taken into account (Legendre 1993). this phenomenon is called spatial autocorrelation, that is, values of variables sampled in neighbor sites are not independent of each other (Tobler 1970), violating the assumption of

independence between samples of the statistical models. Moreover, if there is spatial autocorrelation in the models, it will also lead to spatial autocorrelation in the residuals (Dormann et al. 2007). Thus, in order to avoid this spatial bias in the models, we performed a Moran *I* test, which describe spatial autocorrelation in the data applied in the residuals of a regression between MPD and MFD significant values, and environmental variables. This was performed by the function of the spdep R package (Cliff & Ord 1981). In our case, we did not find a significant spatial autocorrelation in the residuals of the regression model (MPD= Moran I = -0,758; p = 0,50; MFD= Moran I= 0,937, p = 0,46).

We also selected the single best predictive model with its respective set of environmental variables using a Stepwise Model Selection Model based on corrected Akaike information criteria (AICc) (Burnham 2004, Anderson et al. 2012), through the functions of the Mass R package (Venables & Ripley 2002). We used Generalized Linear Models approach (GLM), expressed by the adjusted R<sup>2</sup> statistic (R<sup>2</sup><sub>adj</sub>; Dray et al. 2006), to obtain the variance of MPD and MFD explained by each environmental predictor. We also used the Hierarchical Partitioning (Walsh & Mac Nally 2004, Walsh et al. 2013) to evaluate the independent and joint contributions of each environmental predictor, using the functions of the hier.part R package (Walsh & Mac Nally 2004). Hierarchical partitioning is a method which employs goodness of fit measures (i.e., Log-Likelihood in our multiple regression setting), using all combinations of N variables present in the models tested and compare it to the equivalent model without each analyzed variable (Mac Nally 2002, Walsh & Mac Nally 2004).

# RESULTS

We recorded 25 anuran species (20.762 individuals) belonging to four families (i.e., Hylidae, Leptodactylidae, Microhylidae, Bufonidae) and 12 genera (Fig. 2). The total diversity of traits based on the Rao quadratic entropy was 0,135 for sampled tadpoles. Furthermore, tadpoles trait diversity were concentrated in a few nodes in the phylogeny tree (Fig. 4; single-node skewness test, observed value = 0.190, p = 0.004; few nodes skewness test, observed value = 0,307, p = 0,001). Additionally, the tips skewness test revealed that trait diversity are concentrated near the root of the phylogeny tree (Fig. 4; observed value = 0,420, p = 0,001). As the trait diversity was concentrated in few nodes and close to the root of the phylogeny, we conclude that traits of anuran tadpoles from coastal plains studied here are phylogenetically conserved (Fig. 4).

MPD values of the tadpole communities ranged between -2,18 to 0,57 (mean =  $-1,06 \pm 0.51$ ). Among the 33 tadpole communities sampled, only one showed a positive MPD value which would indicate phylogenetic overdispersion, but it was not significant, i.e. no different than values expected from random assemblages. On the other hand, 18 communities (approximately 55%) showed a significantly phylogenetic clustered structure, that is, species in these communities are more closely related than expected by chance. The 14 remaining communities had non-significant negative MPD values, but indicate the tendency of communities to show phylogenetic clustering (Fig.1).

Moreover, MFD values of the tadpole communities, ranged between -4,38 to -1,45 (mean=  $-2,07\pm0,89$ ). Among the 33 tadpole communities sampled, 12 communities (approximately 37%) showed a significantly functional structure aggregated, that is, species

in these communities are more functionally similar than expected by chance. The 21 remaining communities had non-significant positive MPD values, but suggest a tendency of communities to show a functional structure aggregated. Is worth to note that out of the 12 communities with a functionally aggregated structure, 10 assemblages also showed a clustered phylogenetic structure.

We selected the best model through stepwise model selection based on AICc, with the set of environmental variables that better fit the MPD and MFD values of each community. Among 11 environmental predictors measured here, the best environmental model to MPD included six variables: presence of potential fish predators, internal and external vegetation diversity, canopy cover, dissolved oxygen and water conductivity (Table 2 and 3). The overall model with these six variables explained % (R<sup>2</sup>adj= 0.58) of the total variance of phylogenetic structure (Fig. 5). The most important environmental variables in the GLM model were the presence of potential fish predators, followed by water conductivity, external vegetation structure diversity, canopy cover, internal vegetation structure diversity and oxygen dissolved (Fig. 5). Additionally, water conductivity, canopy cover and internal and external vegetation diversity and dissolved oxygen were negatively related with the MPD values, while the presence of potential fish predator was positively related (Fig. 5).

On the other hand, the best environmental model to MFD, selected trough stepwise model selection based on AICc, contained 5 variables: external vegetation diversity, canopy cover, area, dissolved oxygen and presence of potential fish predators (Table 2 and 3). Remarkable, four variables was correspondingly significant to SES.MDP. The overall model with these five variables explained 41% (R<sup>2</sup>adj= 0.41) of the total variance of functional structure (Fig. 6). The most important environmental variables in the GLM model were the external vegetation diversity, followed by canopy cover, dissolved oxygen and presence of potential fish predators (Fig. 6). Finally, external vegetation diversity, canopy cover, dissolved oxygen were negatively associated with the MFD values, while the presence of potential fish predator was positively associated.

#### DISCUSSION

Our general aims in this study were to investigate the phylogenetic and functional structure of tadpoles' communities from coastal plains in Southeastern Brazil and its relationships with environmental variables. As stated by our predictions, we found a clustered phylogenetic structure in most of the sampled ponds (18 from the 33 analyzed communities). Then, we suggest that clustered phylogenetic structure is a common pattern for the tadpole communities in the coastal plains of the Atlantic forest. Furthermore, our results showed that 12 communities were composed by species more functionally similar than expected by chance, and 10 of theses communities also displayed a clustering phylogenetic structure, signifying that are factors that are probably acting on the species' functional traits and reflecting on the phylogenetic structure, and thus, indicating a strong association between functional traits and the phylogenetic history of species in the study region, which were examined and will be further discussed in this section.

Specifically, we found 2 best environmental model to MPD and MFD included, respectively, six and five ecologically variables, important to anuran tadpoles. Thereby, we

discuss particular influences of these variables on the phylogenetic and functional structure and associating it with the presence and absence of species in the sampled communities.

The presence of potential fish predators was the most important variable and the only positively related the clustered phylogenetic structure (MPD) of the ponds studied here, although the less important but also positively related to functional structure (MFD). It is long well-known the influence of predation in the diversity and distributions of organisms (Paine et al. 1966). Additionally, it is also recognized that predators can cause prey to modify their behavior, morphology, life history, and physiology in an attempt to reduce the risk of predation (Sih 1987, Lima & Dill 1990, Tollrian & Harvell 1999, Relyea et al. 2000, Relyea 2002b). For tadpoles in particular, fish predator can negatively affect their development, grown, and induce morphological changes; these effects on preys can be regarded as adaptive responses to the presence of the predators (Relyea et al. 2000, Relyea 2002b, c). And it could also reduce interspecific prey competition, for instance, reducing or extinct entire populations of strong competitors, leaving an empty niche's space to other more competitively weaker species, in the community (Morin 1983, Relyea 2002a).

Additionally, some studies reveal that aquatic predators selected preys nonrandomly regarding the prey morphology (Relyea 2002c, Van Buskirk & Relyea 1997). As we found, the increase of the presence of potential predator was associated with the increase of the clustering of the phylogenetic structure, thus the potential predators are, seemingly, restraining the occurrence the occurrence of tadpoles species or even determined lineages, like Microhylids' species. However, it is apparently favoring the occurrence of Bufonids' species, possibly a reflection of specific defense that many species of this genera displays, such as cutaneous and body fluids toxins presents in several Bufonids' species.

The water conductivity is a prominent explanatory predictor for taxonomical and functional diversity of anuran tadpoles (Pires et al. in prep) and it was the second more significant explanatory variable to phylogenetic structure. It is known that water conductivity can be a surrogate to food availability or productivity in a pond, as the higher productivity provide more hydrogen ions, and thus a higher conductivity (Moss 2009). And as the higher the productivity, higher will be the availability and quality of food resources (i.e., periphyton). In turn it will generates an increase of species performance in aquatic community, biological aspect commonly associated with certain species' traits, such as traits related with caudal and oral morphology of tadpoles (Waide et al. 1999, Skelly et al. 2002, 2005, Schiesari 2006). Thus, the increase of conductivity may indirectly favors the occurrence of certain lineages, for instance, the Microhylids that was restrained from higher conductivity ponds sampled here. We then suggest that this variable is a relevant predictor phylogenetic clustering on anuran communities.

We also found an important influence of external vegetation diversity to MPD, and it was the most important variable to the MFD. This variable probably determines the availability of suitable sites for vocalization, amplexus, and oviposition for the anuran species, as this complex variable actually interact with species traits in ponds. Thus, the external vegetation structure diversity of a pond is expected to affect directly the distribution and reproduction of anuran clades, (Gascon 1991, Moreira et al. 2010, Wassens et al. 2010, Silva et al. 2011), particularly *Hypsiboas* sp. and *Scinax* sp., species found in this study more abundant in with ponds with higher diversity structure vegetation. Moreover, the canopy cover was the fourth most important explanatory variable to phylogenetic structure and second more important to the functional structure. In fact, canopy cover is claimed to indirectly drive species diversity, and also the growth and development of tadpoles in aquatic habitats, because, open-canopy ponds have higher productivity, and as discussed here, such ponds with higher productivity have higher resource availability and quality (Werner & Glennemeier 1999, Skelly et al. 2002, 2005, Werner et al. 2007). Also, is worth to point out that canopy cover is demonstrated to be an important predictor to functional and phylogenetic beta diversity (Pires et al. in prep). In the sampled ponds of coastal plains, this variable was positively associated with MDP, indicating that ponds with more closed canopies show greater phylogenetic clustering. Thus, as found in this study, segregating forest interior clades, such as Microhylids, from open area clades, as *Dendropsophus* and *Hypsiboas* genera.

Additionally, the internal vegetation structure diversity was the fifth explanatory variable selected. Furthermore, internal vegetation structure diversity is revealed to be an important descriptor to functional, taxonomical and phylogenetic beta diversity (Pires et al. in prep). As external vegetation structure diversity, this predictor is vital to anurans, providing suitable sites to vocalization, amplexus, oviposition, and even predator protection to adults and tadpoles (Gascon 1991, Kopp et al. 2006, Moreira et al. 2010, Wassens et al. 2010, Silva et al. 2011). Therefore, the increase in the heterogeneity of the overall vegetation structure on ponds, such as higher presence of shrubs and trees, may be favoring the presence of certain species, such as species of Hylidae family. Hylids are the most representative family in our study region and they use mainly the vegetation as vocalization sites (Wells 2007, Cardoso & Andrade 1989, Silva et al. 2012a). Since they have adhesive

disks, a key trait to anurans which allows the exploration of three-dimensional habitat (Wells 2007), the vegetation structure must influence the occurrence of species' clade. Therefore, both higher external and internal vegetation structure can directly affect the phylogenetic structure of tadpole communities, as in this study, favoring the occurring of, certain Hylids, such as *Hypsiboas* sp. and *Dendropsophus* sp., in the sampled ponds.

Furthermore, the dissolved oxygen in water (DO) was the sixth more important explanatory predictor to the variance of MPD in coastal plains but the fourth more important to MFD. This variable is a recognized physical parameter of water which has a strong influence on species-specific performance and survivorship of tadpoles (Wassersug & Seibert 1975, Noland & Ultsch 1981, Ultsch et al. 1999, Schiesari 2006). Thus, it could be affecting the presence of species of distinct lineages, such as Rhinella genus, which doesn't have functional lungs in early larval stages (Noland & Ultsch 1981). However, the impacts of long-term hypoxic conditions on growth and development of tadpoles are not well understood (Skelly et al. 2002).

Lastly, the area or surface area was the third more important explanatory variable to the functional structure in anurans' communities in studied coastal region. Physical parameter of water bodies is known to influence the diversity and distribution of tadpoles, but in a complex way. The Island Biogeography theory (IBT) predicts that species richness increase with island size at a certain distance from a source of colonizers. However, stream's volume (a variable strong related with the surface area) was negatively but weakly associated with the tadpoles' richness (Eterovick & Barata 2006), the inverse of the prediction of IBT, if we consider water bodies as islands within a land habitats matrix. But, the increase-surface-area-to-volume ratio was also positively associated with the fitness of *Bufo americanus*. Likewise, in coastal plains ponds, *Rhinella ornata* was more associated with ponds with higher surface area, while *Aplastodiscus eugenioi*, a typical stream`s tadpole species, and *Scinax perpusilus* was more associated with smaller ponds.

In summary, our best predictors were, mainly, negatively related with the MPD and MFD, indicating that the decreased of these variables values, generally, is associated with an increase of clustering in the functional and phylogenetic structure. In other words, the ponds which have lower complexity or heterogeneity present more species closely related than expected from random assembly. Therefore, as we also revealed that the species traits are phylogenetically conserved, these environmental variables should be acting as environmental controls for tadpoles, particularly for the phylogenetic structure. Acting like filter, these variables seemingly to be restraining the presence or the survivor of certain species or even lineages by acting in association with the species' traits, restricting or favoring its occurrences.

In this perspective, these variables appears to be acting particularity in some clades, limiting it occurrences, such as Micriohylids or Bufonids, as favoring the occurrence of another such as Hylids, setting assembly rules to the tadpole's communities, interacting with the functional traits and thus reflecting in the functional and phylogenetic structure in costal plains' ponds, as we found, were clustered or showed a tendency to clustering, in most of the sampled ponds. Our study provided an important step in order to the understanding of anurans phylogenetic and functional structure. The anurans assemblages, by all indications exhibited here, demonstrates to be the outcome of the interactions between ecological and evolutionary processes, as the environmental filtering and the phylogenetic conservation of traits, respectively, in the coastal plains of the Atlantic forest, Southeastern Brazil.

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## TABLES

Table 1. Environmental variables recorded in 33 ponds sampled in coastal plains of Atlantic

Forest, Southeastern Brazil.

Variable	Parameter description
Hydroperiod	Ephemeral pond: retained water by less than the sample period;
	Temporary pond: retained water during all sampling period but less than 100% of the year;
	Permanent pond: retained water during all sampling period and 100% of the year.
Area	Surface area of the pond (m <sup>2</sup> )
Water depth	Maximum depth of the pond (cm)
Canopy cover	Percentage of the canopy cover above the pond
Internal vegetation structure diversity	Percentage of each vegetation types presents in the pond (macrophytes submerged, floating and upright herbaceous, shrubby and arboreal vegetation)
External vegetation structure diversity	Percentage of each vegetation types presents around the pond (upright herbaceous, shrubby and arboreal vegetation)
Presence of potential Fish predator	Determined by collect by a dipnet:??
	Absent (0) or Presence (1)
рН	Water pH
Oxygen dissolved	Water dissolved oxygen level (ppm)
Water conductivity	Conductivity level of the water $(\mu s/cm)$
Water temperature	Temperature of the water (°C)

Table 2. Model Selection results for predicting the **phylogenetic structure** of anurans' communities in coastal plains of Atlantic Forest in southeastern, Brazil. (\* highlighted, the best explanatory environmental model fitted)

Predictive models for MPD	Number of parameters	Ν	AIC <sub>c</sub>	$\Delta_{i}$
Hydroperiod, PP, EVD, IVD, canopy cover, DO, pH, water temperature, water conductivity, surface area and water depth	11	18	8.19	-
PP, EVD, IVD, canopy cover, DO, pH, water temperature, water conductivity, surface area and water depth	10	18	6.73	1.46
PP, EVD, IVD, canopy cover, DO, water temperature, water conductivity, surface area and water depth	9	18	5.42	1.31
PP, EVD, IVD, canopy cover, DO, water temperature, water conductivity and water depth	8	18	3.57	1.85
PP, EVD, IVD, canopy cover, DO, water temperature and water conductivity	7	18	1.92	1.65
PP, EVD, IVD, canopy cover, DO and water conductivity*	6	18	0.89	1.03
$R^2$ of the best model fitted= 0,57				

Table 3. Model Selection results for predicting the **functional structure** of anurans' communities in coastal plains of Atlantic Forest in southeastern, Brazil. (\* highlighted, the best explanatory environmental model fitted)

Predictive models for MFD	Number of parameters	N	AIC <sub>c</sub>	Δ <sub>i</sub>
Hydroperiod, PP, EVD, IVD, canopy cover, DO, pH, water temperature, water conductivity, surface area and water depth	11	12	39.19	_
PP, EVD, IVD, canopy cover, DO, pH, water temperature, water conductivity, surface area and water depth	10	12	37.34	1.85
PP, EVD, canopy cover, DO, pH, water temperature, water conductivity, surface area and water depth	9	12	35.76	1.58
PP, EVD, canopy cover, DO, water temperature, water conductivity, surface area and water depth	8	12	33.83	1.93
PP, EVD, canopy cover, DO, water conductivity, surface area and water depth	7	12	32.36	1.47
PP, EVD, canopy cover, DO, water conductivity and surface area	6	12	31.01	1.35
PP, EVD, canopy cover, DO and surface area *	5	12	29.9	1.11
$R^2$ of the best model fitted= 0,41				

## FIGURES



Figure 1. Sampling area in the coastal plains of Atlantic Forest in São Paulo state. Phylogenetic clustered communities are represented by red circles in sampled ponds (circles), while phylogenetic randomly communities are represented by grey circles.



Figure 2. Phylogenetic relationships of the anuran species recorded in the coastal plains of São Paulo state, Southeastern, Brazil. Species families are indicated on the right. Divergence times estimated from Wiens et al. (2011).



Figure 3. Morphological features measured from tadpoles for calculation of the ecomorphological attributes. Body width (BW), musculature caudal width (MCW), height of caudal musculature (HCM), height of dorsal fin (HDF), height of ventral fin (HVF), body length (BL), body height (BH), spiracle's height (SH), and body total length (BTL).



Figure 4. Decomposition of the trait diversity from sampled tadpoles among the nodes of the phylogenetic tree. The circle's size is proportional to contribution (%) of each node to the total trait diversity.



Figure 5. Hierarchical partitioning of the independent effects of the six best environmental drivers, selected by stepwise model selection based on AICc, to the variance of *phylogenetic structure* (MPD) of anuran communities. PP= presence of potential fish predator, EVD = external vegetation diversity, IVD= internal vegetation diversity, DO=dissolved oxygen; \*denotes positive correlation with the response variable.



Figure 6. Hierarchical partitioning of the independent effects of the four best environmental drivers, selected by stepwise model selection based on AICc, to the variance of *functional structure* (MFD) of anuran communities. PP= presence of potential fish predator, EVD = external vegetation diversity, DO=dissolved oxygen; \*denotes positive correlation with the response variable.

# ENVIRONMENTAL AND SPATIAL DRIVERS OF FUNCTIONAL, TAXONOMICAL AND PHYLOGENETIC BETA DIVERSITY OF ATLANTIC FOREST FROGS

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## ABSTRACT

Deterministic theories indicate that niche-based processes, such as interspecific competition and environmental filtering, originate and maintain the diversity in ecological communities. In contrast, stochastic and neutral processes, such as ecological drift and random dispersal, may also be the main process related to local community structure. Herein we assess the spatial and environmental correlates of the different components of diversity of anurans tadpoles in coastal plains of Southeastern Brazil, including functional (FD), taxonomical (TD), and phylogenetic (PD) beta diversities. We performed a distance-based redundancy analysis (db-RDA) to partition the explained variance of anuran beta diversity by the environmental and spatial predictors models selected. The spatial predictors were the most important explanatory variables, explaining larger fractions of the variance of anuran beta diversities (FD=22%; TD= 14%; PD=16%). Our results demonstrate the importance of spatial processes, such as dispersal limitation, to structure the beta diversities of amphibians in the study region. Although less important, the environmental variables, such as water conductivity and vegetation structure, were also significant predictors of beta diversity (FD=12%, TD= 13%; PD=5%). All selected environmental variables influenced the performance and the occurrence of species in communities, reflecting the implication of environmental-based processes in anuran beta diversities. We found a similar spatial structure of **TD**, **FD** and **PD**, as well as the environmental structure. This encounter may indicate that although we are assessing different components of beta diversity, similar or even the same processes originated and are maintaining the anuran beta diversities in the studied region. Finally, the strong spatial structure in beta diversities found here, was consistently with another amphibians communities and other aquatic organism such as fish

and macroinvertebrates, evidenced the significance of spatial processes, such dispersalbased process, to structure aquatic communities.

KEYWORDS: community ecology, beta diversity, aquatic communities, dispersal-based processes, niche-based processes, tadpoles, amphibians, coastal plains

#### **INTRODUCTION**

Why biodiversity is non-randomly distributed through space? What defines the structure and patterns of biological diversity in ecological metacommunities? These are some of the key questions in ecology. Hutchinson (1959) formally proposed similar questions, asking to himself why there are so many animal species in the world. Since then, a myriad of questions involving the factors which originated and are responsible for the distribution of biodiversity have emerged.

In order to properly answer these questions, we first must understand how biodiversity can be expressed and described. In this sense, we can decompose biodiversity in three main components: the taxonomic, phylogenetic, and functional diversity (De Bello et al. 2010). The first one regards the richness and relative abundance of species in a given community; this is the classical measure of the diversity. The second take into account the evolutionary history shared by species occurring in the community, expressed as phylogenetic diversity (Faith 1992, Cadotte et al. 2010, De Bello et al. 2010). The last one corresponds to the phenotypic traits' diversity of species in the community (Ricotta 2005).

The spatial component of biological diversity can be described by the concept of  $\beta$  diversity (Whittaker 1960), expressed, for instance, by pairwise differences of biodiversity between local communities (De Bello et al. 2010). The understanding of the  $\beta$  diversity patterns and their underlying processes is a crucial step to better comprehend what factors originate and maintain the biodiversity (Legendre and De Cáceres 2013).

The spatial variation between ecological communities, or the  $\beta$  diversity, emerges as the outcome of different processes occurring at distinct scales of space and time, asymmetrically acting in the assembly of each community, e so generating a compositional variation between them. For instance, niche's theories indicate that niche-based processes, such as interspecific competition (e.g. Macarthur and Levins 1967, Diamond 1975) and environmental filtering (e.g. Lebrija-Trejos et al. 2010), could determine the presence and absence of species in each community. In contrast, stochastic and neutral processes, such as ecological drift and random dispersal, could be also related to the local community diversity and thus the spatial variation among these communities (Hubbell 2001). In broader scales, the metacommunity diversity could be a result of historical and evolutionary processes such as speciation, extinction and dispersal (*sensu* Platnick, 1976) of lineages (Ricklefs 2008). Furthermore, these processes can mutually influence the regional species pool from which local communities are assembled (Ricklefs and Schluter 1993, Wiens and Donoghue 2004).

We could start to investigate these processes by understanding what predictors better explain the variation of biological diversity observed between assemblages within a metacommunity. One of the predictors most commonly used correspond to a set of environmental variables related to the species' habitat use, because traditional niche theories state that there are a strong relationship between environment and species' features, such as phenotypic traits (Tilman 1982, Tokeshi 2009). This relationship could regulate the niche overlapping of species and consequently determine their presence or absence in a given assemblage (Macarthur and Levins 1967b, Tilman 1982, Tokeshi 2009). Additionally, owing to the spatial nature of several processes (i.e., neutral and niche based processes) structuring the variance within metacommunities, spatial predictors have been recently used as a proxy to disentangle the influence of such spatially structured processes (Keitt et al. 2002, Cottenie 2005, Dray et al. 2012).

Owing to the complex biological nature of ecological communities, ecologists often choose one taxonomic group of interest to investigate underlying processes related to the structure of biological communities (Magurran 2004). The Neotropical anuran amphibians correspond to an excellent study model among vertebrates to investigate the roles of ecological, evolutionary, and spatial structure of ecological communities. They exhibit high species diversity (942 species in Brazil; Segalla et al., 2014), and shows both broad and narrow geographic distributions (IUCN 2013, Jenkins et al. 2013). Moreover, this variation in the distributional patterns of anurans is often suggested to be a response to ecological, spatial and evolutionary mechanisms, such as environmental control and dispersal limitation. It can happens because amphibians are extremely influenced by these mechanisms, owing, for instance, to the their phenotypic and behavioral traits' variability, their complex life cycle and permeable skin (Haddad and Prado 2005, Becker et al. 2007, Keller et al. 2009, Silva et al. 2012b, Valdujo et al. 2013).

Several studies have evaluated the mutual influence of ecological and spatial processes on community variance structure, consistently testing environmental and spatial predictors that best explain patterns of diversity (e.g. Sokol et al. 2013, 2011, Prado and Rossa-Feres, 2014). However this framework remains to be applied consistently for amphibian, particularity exploring the beta component of diversity. Still, this approach is becoming increasingly important in order to understand the origin and maintenance of beta diversity (Legendre et al. 2005). Thus we performed herein a variation partitioning approach to assessing the relative influence of spatial and environmental predictors on

taxonomical, phylogenetic and functional beta diversity of tadpoles in the coastal plains of Southeastern of Brazil.

Based on their particular biological features of anurans, such as complex life cycle or phenotypic and behavioral variability, which is demonstrated by a number of studies to be influenced by environmental and spatial predictors, we tested the following predictions: (1) as anurans have an limited dispersal (cf. Smith and Green 2005), which makes the spatial structure to be the predominant predictor in different components of beta diversity, particularity for taxonomical, and phylogenetic diversities; but (2) as the functional traits have a strong relation with the environmental, we expect that environmental heterogeneity is the main predictor in the functional diversity.

#### MATERIAL AND METHODS

#### Study area

The study area comprehends most of the coastal plains of São Paulo state, southeastern Brazil, which includes four natural geomorphological units as proposed by Suguio and Martin (1978) (Appendix 1 and Fig. 1). This region comprehends about 550 km of extension and is naturally bounded by its particular geomorphological history. The coastal plains of this region are bounded on southern and northern portions by Precambrian basements of the Serra do Mar range (Suguio and Martin 1978, 2013). Moreover, this region is naturally divided by narrow headlands of Precambrian rocks (Suguio and Martin 1978).

Climate of the study region is of the type Af, following the Koppen climate classification (Peel et al. 2007), with mean annual precipitation ranging between 1800 and 2000 mm, mean minimum temperature of 19°C, and mean maximum temperature of 27°C (Melo and Mantovani 1994). The vegetation is composed by herbaceous, shrubs and forest formations on the coastal plains, classified as "restinga" forests and ombrophilous lowland forests, belonging to the Atlantic Forest's domain (Marques et al. 2011), . These formations are heterogeneous, being variable in canopy height, hydric saturation of the soil, and the distance from the Serra do Mar slope (Fig. 1). This heterogeneity depends on extent of the coastal plains and the characteristics of sandy soils. Moreover, it suffers the influence of distinct sediments, which arise from the adjacent scarps and streams (Klein 1961, Mantovani 2000).

## Biological surveys

We sampled 37 ponds distributed along coastal plains of São Paulo state, southeastern Brazil (Fig 1). The tadpoles and their potential fish predators were sampled in the ponds through swap with a dipnet (30 cm of diameter with 3 mm<sup>2</sup> of mesh) in all suitable microhabitats available to the tadpoles. The specimens were collected and determined by species level in the laboratory. Specimens were housed at Coleção Científica de Anfíbios - Girinos, do Departamento de Zoologia e Botânica da UNESP, São José do Rio Preto - DZSJRP. Each pond were swept during one hour-pond and sampled in three different occasions between October 2011 and April 2012, totaling a sampling effort of 111 hours-person in all ponds.

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The composition of species sampled in the study area was utilized by us to construct a "community composition matrix", in which the species was represented in columns and the communities sampled in the rows. As the tadpoles' abundance is understood to be much more a consequence of each species' reproductive modes and strategies instead of spatial and environmental influence (Well 2007, McDiarmid and Altig 1999), we chose to use only the presence and absence of species in the communities, to compute the community composition matrix.

### ENVIRONMENTAL DATA - sampling and processing

The follow environmental variables were collected in all sampled ponds (see Table 1 for details): area, hydroperiod, water depth, internal and external vegetation structure diversity, canopy cover, presence of potential predator (fish), pH, water temperature, water conductivity, and oxygen dissolved level. The canopy cover proportion was measured with Spherical Crown Densiometers. The pH and water conductivity was measured in with a Extech® ExStik pH Pen. The water temperature and oxygen dissolved levels were measured in an YSI DO 200 Oxygen Meter. The categorical variable, hydroperiod were coded as dummy variables (Bocard et al. 2011). For numerical continuous variables (water depth, area, water temperature, water conductivity, and oxygen dissolved level), we applied the natural logarithm, standardized by the range of variables, and subtracted the maximum by the minimum value of each variable, as suggest in Pavoine et al. (2009). In this way, all numerical variables had the same weight in the analysis.

We have not found multicoliarity between environmental variables based on Pearson correlation matrix (r <60%, a reasonable correlation threshold). Therefore, all environmental variables were considered in data analysis. We performed a Stepwise Model Selection based on AICc, which selects the set of environmental variables [E] that better explain the variance on beta diversities (Burnham and Anderson 2002), using functions of the stats R package (Hastie and Pregibon 1992).

## PHYLOGENETIC DATA - sampling and processing

We used the phylogenetic hypothesis proposed by Pyron and Wiens (2011) for the phylogenetic diversity measures. We constructed a tree based on this phylogenetic hypothesis, including only our regional pool of species. We assigned age estimates for all nodes based on Wiens et al. (2011). We added species absent in the original phylogeny of Pyron and Wiens (2011), using the functions in phytools R package (Revell 2012). We estimated tree branch lengths through the BLADJ algorithm of the Phylocom 4.1 software (Webb et al. 2008). This algorithm was used to evenly interpolate ages of dated nodes to non-dated nodes. The phylogenetic tree for the regional pool was computed using phylomatic tool in Phylocom 4.1 software (Webb et al. 2008), which pruned the tree in order to include only species from the regional pool considered here. The regional pool was composed by all species recorded in the Serra do Mar costal forest (see Rossa-Feres et al. 2011).

### TRAIT DATA - sampling and processing

To calculate functional diversity, we measured phenotypic traits from two to five individuals of each species collected, depending of the number of specimens available for each species (Table 2). We have taken the follow quantitative morphological measures from tadpoles, in order to obtain ecomorphological traits: body width (BW), musculature caudal width (MCW), height of caudal musculature (HCM), height of dorsal fin (HDF), height of ventral fin (HVF), body length (BL), body height (BH), spiracle's height (SH), and body total length (BTL). We then calculated five ecomorphological traits which potentially represent the habitat use of Neotropical tadpole species (McDiarmid and Altig 1999), based on means of the following index: caudal relative height (CRH = (HCM + HDF + HVF)/BH); body compression (BC = BH/BTL), relative width of caudal musculature (RWCM = HCM/ MCW), relative caudal length (RCL = BL/BTL), and relative spiracle's position (RSP=SH/BH). We also included the follow categorical measures: oral opening (OR), number of denticle rows (NDR), flagellum presence (FP), spiracle's position (SP), eye's position (EP), and body shape (BS). The selection of traits was based on the strong association between them with ecological and biological features such as habitat use, foraging behaviors that can influence the ecosystem structure and specific defense against predation (Semlitsch 1990, McDiarmid and Altig 1999, Wassersug 2000, Van Buskirk 2002, Strauß et al. 2010, Both et al. 2011). Finally, all index and measures were used to construct a pairwise distance matrix of species' traits, based on the "Gower" dissimilarity for mixed variables (FDM) (Legendre & Legendre, 2012, see Fig. 3 for details of traits).

#### SPATIAL DATA – processing data

We performed a spatial eigenfunction analysis in order to obtain spatial predictors and to describe the spatial structure of tadpoles' beta diversity (Griffith and Peres-Neto 2006, Legendre and Legendre 2012), based on Moran Eigenvector Maps (MEMs, see Dray et al., (2006). MEMs are eigen-decompositions of spatial weighted matrices which generate orthogonal vectors used as spatial predictors in multivariate analyses (Dray et al. 2006, Legendre et al. 2012).

Moreover, MEMs could describe multiscale spatial structures ranging from fine to global spatial scales, and enable us to understand which scales are more important to describe the spatial structure of response variable (in our case, **FD**, **TD** and **PD**); so we can define submodels that represent different spatial scales and their associated MEMs (Dray et al. 2006). The definition of submodels is commonly defined according to ecological hypotheses of interest and their spatial interactions of a given study, and also by the similarity in the periodicity of spatial structure of significant MEMs (Ali et al. 2010, Legendre et al. 2012). We then inspected visually each significant MEM to define the submodels of spatial structure of our study region. Two submodels were defined representing global and fine spatial structure (see examples in Fig. 4) based on the visualization of MEMs and the graphics of similarity in the periods or modulation between MEMs. These two scales can represent ecological processes spatially structured at different scales, such as environmental control, dispersal, and interspecific competition.

An essential step in the MEM approach is the definition of a neighborhood matrix, which describes spatial relationships among objects (Dray et al. 2006). In our case, it is necessary to define which samples (i.e., ponds) are neighbors and which are not. We used a heuristic approach assessing several neighborhood distances between ponds, beginning by the distance obtained through minimum spanning tree algorithm (110.98 km) up to a maximum distance between ponds (287.52 km). The best neighborhood matrix and the set of MEMs were selected based on corrected Akaike information criteria using functions of the spacemakeR R package (Dray et al. 2006).

We also performance a Model Selection based on AICc using the MEMs as explanatory variables to evaluate which spatial variables (MEMs) was associated with the environmental variation between communities (response variable). The MEM 13 (functional beta diversity); MEM 1 and 19 (taxonomical beta diversity); and MEM 13 and 36 (phylogenetic beta diversity) were selected as best spatial descriptor for the environmental variation between communities and thus retained from the future analyzes to better comprehension of the relative real importance of predictors. The remaining MEMS selected but not associated with the environmental were used as the potential spatial predictors [E] for the analyzed beta diversity components in this study (Table 2).

## DATA ANALYSIS

#### *Measuring beta diversity*

We calculated the taxonomic, phylogenetic, and functional diversities to obtain the beta component of tadpoles' diversity, using the Rao quadratic entropy index, based on the framework proposed by De Bello et al., (2010). According to this framework, the corrected version of a Rao index (Jost 2007) is a useful and suitable metric to estimate diversity,

because it formally combines different components of diversity (i.e., taxonomic, phylogenetic, and functional). Therefore, the corrected Rao index is particularly important when one aims to compare the taxonomic, phylogenetic and functional diversities. Using these metrics provided by De Bello et al., (2010), we constructed three pairwise distance matrices, namely taxonomic distance matrix (**TD**), using community composition matrix only; the phylogenetic distance matrix (**PD**), which was built via communities composition matrix distance matrix (**FD**), was made using the community composition matrix and the traits matrix. Theses matrices were used as response matrices and represent the beta component of taxonomical, phylogenetic, and functional diversity metrics.

## Assessing the environmental and spatial predictors on beta diversity

We performed a distance-based Redundancy Analysis (db-RDA) to analyze the explained variation of the anuran tadpoles' beta diversities (**TD**, **PD** and **FD**) by the selected environmental [**E**] and spatial predictors [**S**], expressed through the adjusted R<sup>2</sup> statistics (R<sup>2</sup>adj, Peres-Neto et al. 2006). For this propose, we used functions in vegan R package (Oksanen et al. 2013). We then used the variation partitioning approach to assess the shared and unique contributions of spatial and environmental predictors which explained the variation of tadpoles beta diversities (Bocard et al. 1992, Peres-Neto and Legendre 2010). The total variation was decomposed in three fractions, corresponding to variation explained purely by environmental variation [**E** | **S**], spatially structured environmental variation [**E**  $\cap$  **S**], or purely by spatial variation [**S** | **E**] (Borcard et al. 1992). Moreover, the significance of each independent fraction was tested by permutation

functions of the vegan package in R (Oksanen et al. 2013).

## RESULTS

## Anuran fauna

We recorded tadpoles of 25 species of amphibian anurans (N = 21.160 individuals) belonging to four families and 12 genera (Table 2 and Fig. 2). The family with the highest observed richness was Hylidae (19 species), followed by Leptodactylidae (three species), Microhylidae (two species), and Bufonidae (one species). The genera with highest richness were *Dendropsophus* and *Scinax* (six species each). The average richness shown by each pond was five species ( $\pm$ 3,0), ranging from one to 12 species (Table 2). Furthermore, *Hypsiboas albomarginatus* (Hylidae) was the most frequent species, occurring in 25 of the 37 sampled ponds, and the second most abundant species (N = 3222 individuals). *Leptodactylus latrans* (Leptodactylidae) was the most abundant species in the samples (5315 individuals recorded), but was recorded only in five sampled ponds.

#### Effects of environmental and spatial predictors on tadpole's beta diversity

Both environmental and spatial predictors were significantly related to the three components of beta diversity (P<0,01). We selected through corrected Akaike information criteria (AICc) with the best neighborhood matrix and spatial predictors for each component of diversity (Table 3). The better neighborhood matrices for the tadpoles' beta diversity selected was the distance-based neighborhood, with fifty neighborhood matrices

tested with different maximum distances to the nearest pond, ranging from 114.5 to 287.52 km, the later corresponding to the maximum distance between sampled ponds in our study. For **FD** was selected one MEM in global scale and four MEMs in fine scales while for TD was selected three MEMs in fine scales, yet for **PD**, 5 MEMs in fine scale was selected (Table 3 and Appendix 1). The environmental models for **FD**, **TD** and **PD**, selected through stepwise model selection based on AICc, include: pH, water conductivity, internal vegetation structure diversity, canopy cover, pH and water depth (for more details, see Table 3).

The variation partitioning showed that 40% the of variation on the functional beta diversity was explained by the full model, whereas 12% were explained by pure environmental predictors, 6% were explained by the environmental predictors spatially structured, and 22% by the pure spatial predictors. Nevertheless, 30% of variation of the taxonomical beta diversity explained by the selected predictors, for which 13% were explained by pure environmental predictors, 3% by the environmental predictors spatially structured, and 14% were explained by the pure spatial predictors. Considering the phylogenetic beta diversity, the full model of environmental and spatial predictors, 5% were explained by pure environmental predictors spatially structured, and 16% were explained by the environmental predictors spatially structured, and 16% were explained by the environmental predictors spatially structured, and 16% were explained by pure spatial predictors (Figure 5).

#### DISCUSSION

We found a strong spatial structure in all three component of beta diversity assessed herein, evidenced through the variance explained by pure spatial components of the tadpoles' beta diversities (**FD**= 22%; **TD**= 24% and **PD**= 16%, for more details, see Figure 5). We found that one spatial predictor was important to explain the variance in the components of beta diversity represent spatial structures in broader scale (i.e. MEM 1 for **FD**, Table 3). However, the major of spatial predictors selected represent the spatial structure at fine scales, which indicates that most of the variation explained by spatial predictors in the beta diversity was structured in fine scale (i.e., MEM 25, 32 and 36 for **FD**, MEM 9, 18, 19 and 21 for **TD** and MEM 4, 6, 11, 17 and 32 for **PD**; see Table 3).

The strong spatial structure encounter here indicates that two main distinct processes might be structuring the three components of tadpoles 'anuran beta diversity and may be interpreted by it. The first explanation would be the effect by the environmental variables which were not directly measured in this study and possibly affect the adults and tadpoles, such as humidity levels, rainfall or food availability, but as they may be spatially structured, its effects and relative explanation of beta diversity variance can be represented by the pure spatial component (Beisner et al. 2006, Nabout et al. 2009, Diniz-Filho et al. 2012).

On the other hand, pure spatial effects could indicate the influence of neutral processes, for instance related with random dispersal of species. Neutral theory postulates that similarity between sites decrease with increasing of geographic distance, generating spatial structure in beta diversity related to random dispersal (Hubbell 2001, Diniz-Filho et

al. 2012, Tuomisto et al. 2012). Diniz-Filho et al. (2012) found that spatial component explained 18.5 % of anuran beta diversity in communities from Amazonia, which were consistent with neutral predictions based in their comparison of simulated communities structured exclusively by neutral dynamics. However, besides their low dispersal ability (Smith and Green 2005), and considering the clear influence of environmental variables in habitat selection and distribution of anurans (e.g. Becker et al. 2007), would be more parsimonious to interpret that both niche and neutral processes can simultaneously affect anuran beta diversity (Gravel et al. 2006) although in distinct ratios, as showed in this study. For instance, the dispersal limitation of anurans prevents species to reach suitable habitats and, consequently, determine the tadpole's distribution (Cottenie and De Meester 2004, Bie et al. 2012). Then, we suggest that dispersal of anurans would be an important mechanism to generate patterns of functional, phylogenetic and taxonomical beta diversity in the Atlantic Forest.

Although spatial predictors have been more important to describe the functional, phylogenetic and taxonomical beta diversity in our study, the environmental variables sampled and then selected by our analysis, were also significantly relevant to explain the variation in the three components of beta diversity, as evidenced by the pure environmental fraction (**FD**= 12%; **TD**= 13% and **PD**= 5%, for more details, see Figure 5) and the fraction of environmental possibly spatially structured (**FD**= 5%; **TD**= 3% and **PD**= 5%, for more details, see Figure 5) of the explained variance. Anurans are particularity affected both directly and indirectly, by environmental conditions (see Becker et al., 2007; Silva et al., 2012a; Wilbur, 1987). In worth to note that for TD, both, environmental and spatial predictors were similarly important, differing by approximately 1% (Figure 5).

These variables influence several aspects of the biology of amphibians, including reproductive modes and phylogenetic diversity (Silva et al., 2012b). Furthermore, environmental predictors are commonly used to infer niche-based processes, considering the strong relationship between species distributions and determined environmental variables (Tuomisto and Ruokolainen 2006). Thus, assessing the strength of the relationship of environmental variable and beta diversity, as well as the presence and absence of the species in the communities, may shed light into begin to understand the effects of niche-based processes on the spatial variation of tadpole's diversity. Thus, in this section, we will discuss the importance of each environmental variable to amphibians' biology and ecology aspects in association with its occurrence in coastal plains ponds.

The most important environmental variable selected as a vital explanatory variable to phylogenetic, taxonomical and functional beta diversity was the same, namely: internal vegetation structure diversity. This is interesting, since these three metrics represent distinct scales of biodiversity (de Bello et al. 2010), but may be reflecting the fact that traits of species determine the ways and strengths of the species interactions between them and the environment, and consequently can produce a spatial variation structure at community level (Welborn et al. 1996). Moreover, it is worth noting that this predictor is very relevant to tadpoles' biology. In fact, this variable was an important predictor to phylogenetic structure of anurans in the study region (Pires et al. in prep). Moreover, the diversity of internal vegetation structure diversity should affect anuran assemblages by providing sites for vocalization and oviposition to adults, and even protection of tadpoles against predators (Gascon 1991, Moreira et al. 2010, Wassens et al. 2010, Silva et al. 2011). In the ponds sampled here, we found several Hylids, such as *Scinax* sp. and *Dendropsophus* sp.

associated with higher diversity of vegetation structure, which is expected, as this variable is a vital reproductive requirement to these species (Silva et al. 2011, Wells 2007).

Furthermore, other crucial environmental variable to functional and phylogenetic beta diversity, canopy cover is clamed to indirectly drive tadpoles' diversity and their performance in ponds. This variable is an important predictor to phylogenetic and functional structure (Pires, et al. in prep), virtually separating species associated with forest interior such as Microhylids, from open area species, as some Hylids (Wells 2007, Werner et al. 2007), such as the genera *Dendropsophus* and *Hypsiboas*, associations found in this study. The reasoning behind it is that higher productivity in open canopy ponds provides greater resource availability, which can influences anuran diversity and species performance (Skelly et al. 2002, 2005, Schiesari 2006, Werner et al. 2007), and as evidenced here, the phylogenetic, taxonomical and functional beta diversity.

Another vital variable that was selected to be an important predictor to functional and taxonomical was the pH. In fact, pH extremes values can directly influence the development, fitness and the survivor of tadpoles (Leuven et al. 1986, Warner et al. 1991, 1993, Pehek 1995, McDiarmid and Altig 1999). In our case, we found species of Scinax, the genus *Physalaemus* sp., and some families, such as Leptodactylidae and Microhylidae associated to more neutral pH ( $\pm$ 7,0) but excluded from lower pH (< 5.0), so we believe that the pH, when in extreme values, may be influencing the occurrence of some anurans species in coastal plains.

Moreover, an important explanatory variable to taxonomical beta diversity, water conductivity is assumed to be a surrogate of food availability and productivity, and therefore it is also recognized as a key surrogate variable to productivity for aquatic communities (Moss 2009). The reasoning behind that is that, productivity influences directly species diversity, because the increasing productivity may produce a complementarity in the resource use and consequently the occurrence of species (Schiesari 2006, Skelly et al. 2005, 2012). In coastal plains, water conductivity is also an important explanatory predictor for the phylogenetic structure of anuran tadpoles (Pires et al. in prep). Moreover, we have found that certain clades, such as *Dendropsophus* sp. and *Rhinella* sp. associated with higher conductivity, as the Leptodactilids associated with lower conductivity, thus this variable may be indirectly affecting the occurrence of specific clades.

Nevertheless, an important predictor to functional beta diversity, the water depth is related to habitat use of tadpoles, as they are distributed through the water column according to their ecomorphological guilds (Gascon 1991, McDiarmid and Altig 1999, Eterovick and Fernandes 2001, Fatorelli and Rocha 2008) thus, indicating an important association between tadpoles traits and the water column. The ponds that are deeper, for instance, may potentially harbor greater diversity of species and lineages, in our case, we found certain Hylids, such as *Hypsiboas semilineatus*, *Itapotihyla langsdorffii* only associated with deeper ponds. This may happen because, greater microhabitat availability could attenuate the effects of biotic interactions, such as interspecific competition and deeper ponds retains water in dry periods which allows the development of a higher number of species (Alford 1999). Moreover, Both et al (2011) demonstrate that the deeper water was an important predictor for both richness and composition of tadpoles, as apparently deep ponds that retain water even during dry periods provide more microhabitats available

for the development of species. And finally, Crump (1991) demonstrated that the water depth is a key factor for anuran adults to discriminating and selecting their reproduction and oviposition sites, features strongly associated with tadpoles traits, with respect to its reproduction modes (Haddad and Prado, 2005).

Lastly, the presence of potential predator was selected was an explanatory predictor essential to phylogenetic beta diversity. In fact, is worth to point out the this was selected also to be the most important environmental variable explaining the tadpoles phylogenetic structure, and a significant predictor to the functional structure, in coastal plain of Southeastern Brazil (Pires et al. in prep). In this sense, it is recognized the influence of predation in the diversity and distributions of organisms (Paine et al. 1966). For tadpoles in particular, fish predator can negatively affect their development, grown, and induce morphological changes (Relyea et al. 2000, Relyea 2002b, c). And it could also reduce interspecific prey competition, for instance, reducing or extinct entire populations of strong competitors, leaving an empty niche's space to other more competitively weaker species, in the community (Morin 1983, Relyea 2002a).

Another interesting result is that, the increase of the presence of potential predator was associated with the increase of the clustering of the phylogenetic structure (Pires et al, in press), thus the potential predators are, seemingly, restraining the occurrence the occurrence of tadpoles species or even determined lineages, like Microhylids' species. However, it is apparently favoring the occurrence of Bufonids' species, possibly a reflection of specific defense that many species of this genera displays, such as cutaneous and body fluids toxins presents in several Bufonids' species.

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It is worth observing that taxonomical, phylogenetic and functional beta diversity was similarly influenced by spatial predictors, in terms of explained relative variation and spatial scales (most fine-scale). Moreover, environmental variables also seem to affects components of beta diversity in a similar way. For instance, to phylogenetic, taxonomic and functional beta diversity, there are equally important variables, the internal vegetation structure diversity, besides other similar results among other components of beta diversity discussed above. In other words, although we are assessing different components of beta diversity, the spatial predictor strongly influenced all beta diversity components, and even the environmental predictors, despite their not so strong influence, were similar to functional, taxonomic and functional beta diversity, in some matched to one or more components, and even the relative importance of the theses predictor in the variation partitioning (Figure 5). This could indicates that similar or even the same processes, either spatial or niche-based, originated and are maintaining the anuran beta diversity in the studied region.

Overall, the significant spatial structure in anuran beta diversities found in our study was consistent with many other found for aquatic organisms including fishes, macroinvertebrates, zooplankton and even anurans, among others (Johnson and Goedkoop 2002, Beisner et al. 2006, Paavola et al. 2006, Johnson et al. 2007, Prado and Rossa-Feres 2014). The spatial pattern found in these aquatic communities, included the tadpoles communities studied here, points to a significant spatial structure (on a continuum between fine to global scales) of processes, such as dispersal-based processes or niched-based processes, in assembly of communities. Also As evidenced here, it also shows the strengthening importance in assessment of spatial structure of aquatic communities. Our study is an important step in order to reveal the underlying processes driving distinct components of the beta diversity in vertebrate aquatic communities. We also highlight the importance of simultaneous evaluation of the different components of beta diversity and the factors that may influence it, either spatial, or environmental among others, as this assessment could reveal distinct processes that are occurring simultaneously and thus, determining the aquatic communities assembly.

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# TABLES

Table 1. Environmental variables recorded in the 37 ponds sampled in the coastal plains ofSão Paulo state, southeastern, Brazil.

Variable	Parameter description
Hydroperiod	ephemeral: retained water less than the sample period;
	temporary: retained water during all sampling period but less than 100% of the year;
	permanent: retained water during all sampling period and throughout the year.
Area	surface area of the pond (m <sup>2</sup> )
Water depth	maximum depth of the pond (cm)
Canopy cover	Percentage of the canopy cover above the pond
Internal vegetation structure diversity	percentage of each vegetation types presents in the pond (macrophytes submerged, floating and upright herbaceous, shrubby and arboreal vegetation)
External vegetation structure diversity	percentage of each vegetation types present around the pond (upright herbaceous, shrubby and arboreal vegetation)
Presence of potential predator (fish)	determined by visual inspection or collected by a dipnet:
	absent (0) or present (1)
рН	pH of the water inside the pond
Oxygen dissolved	dissolved oxygen in the water inside the pond (ppm)
Water conductivity	conductivity level of the water of the pond ( $\mu$ s/cm)
Water temperature	temperature of the water of the pond (°C)

Table 2. Best explanatory environmental and spatial predictors fitting the three different components of tadpoles' beta-diversity, selected by the stepwise model selection based on AICc (environmental variables) and Model Selection based on AICc (spatial variables).

Functional beta diversity (FD)		
Environmental variables	Spatial variables	
pH, internal vegetation structure diversity, water depth and canopy cover	MEM 1 (global scale) and	
	MEM 9, 18, 19 e 21 (fine scale)	
Taxonomic beta diversity (TD)		
Environmental variables	Snatial variables	
pH, water conductivity, internal vegetation structure diversity and water depth	MEM 25, 32 e 36 (fine scale)	
Phylogenetic beta diversity (PD)		
Environmental variables	Spatial variables	
Internal vegetation structure diversity, canopy cover and presence of potential predator (fish)	MEM 4, 6, 11, 17, 32 (fine scale)	

# FIGURES



Figure 1. Sampling area in the coastal plain of São Paulo state. Sampled ponds (N = 37) represented by red circles.



Figure 2. Phylogenetic relationship of the anuran species recorded in the coastal plains of São Paulo state, Southeastern, Brazil. Families are indicating on the right. Time divergences estimated from Wiens et al. (2011).



Figure 3. Morphological variables recorded for the calculation of ecomorphological attributes: body width (BW), musculature caudal width (MCW), height of caudal musculature (HCM), height of dorsal fin (HDF), height of ventral fin (HVF), body length (BL), body height (BH), spiracle's height (SH), and body total length (BTL).





Figure 4. Examples of global and fine scales of Moran Eigenvector Maps (MEMs). Each square represent the pond sampled in study region. White squares denote negative scores while black squares denote positive scores. This scores values are also represented in each graph below the maps, where is possible to identify similarity in the periods ("modulation") between MEMs. MEM 1 represents spatial structures of beta diversity (in this example, **FD**) in a global scale, while MEM 21 represents spatial structures at fine scale.



Figure 5. Variation partitioning (adjusted  $\mathbb{R}^2$ ) resulting from the distance-based partial redundancy analysis (db-RDA). **FD**=Functional Beta Diversity; **PD**= Phylogenetic Beta Diversity; and **TD**= Taxonomical Beta Diversity. **E** | **S**= pure Environmental; **E**∩**S**= Environmental Spatially structured; and **S** | **E**= pure Spatial.

## APPENDICES







Figure 6.1 All Moran Eigenvector Maps (MEMs) selected as the best model of the spatial structure for **Functional Beta Diversity (FD)**. Each square represent the ponds sampled in study region. White squares denote negative scores while black squares denote positive scores. This scores values are also represented in each graph below the maps, where is possible to identify similarity in the periods ("modulation") between MEMs. The MEM 1 represents global scales while MEMs 9, 18, 19, 21 represents fine spatial structures of **FD**.





Figure 6.2 All Moran Eigenvector Maps (MEMs) selected as the best model of the spatial structure for **Taxonomical Beta Diversity** (**TD**). Each square represent the ponds sampled in study region. White squares denote negative scores while black squares denote positive scores. This scores values are also represented in each graph below the maps, where is possible to identify similarity in the periods ("modulation") between MEMs. All MEMs represents fine spatial scale of spatial structures of **TD**.







Figure 6.3 All Moran Eigenvector Maps (MEMs) selected as the best model of the spatial structure for **Phylogenetic Beta Diversity** (**PD**). Each square represent the ponds sampled in study region. White squares denote negative scores while black squares denote positive scores. This scores values are also represented in each graph below the maps, where is possible to identify similarity in the periods ("modulation") between MEMs. All MEMs represents fine spatial scale of spatial structures of **PD**.

## CONSIDERAÇÕES FINAIS

Na região estudada foram registrados girinos de 25 espécies de anuros, pertencentes a quatro famílias e 12 gêneros. A riqueza média encontrada foi de cinco espécies, com amplitude de 1 a 12 e desvio padrão de três espécies.

Os preditores que explicam a maior porcentagem da variação nas diferentes componentes da diversidade beta estudados aqui (i.e. taxonômica, funcional e filogenética) são as variáveis espaciais. Esses resultados demostram a existência de uma clara estrutura espacial nos diferentes componentes da diversidade beta de anuros nas planícies costeiras da mata atlântica no estado de São Paulo. Isso demostra que na planícies costeiras, os anuros demostram uma clara limitação espacial para a dispersão entre as poças, mostrando que os espaço esta agindo como um filtro para muitas dessas espécies.

Embora um pouco menos importante, as variáveis ambientais aqui selecionadas, tal como a condutividade da água, pH e a estrutura da vegetação, também explicam uma fração importante da variação das diferentes faces da diversidade beta de anuros e demostram a forte influencia de processos baseados em nicho, como o filtro ambiental, na variação da diversidade entre as comunidades estudadas.

As variações da diversidade beta taxonômica, funcional e filogenética dos girinos apresentam uma estrutura espacial semelhante, assim como uma estrutura ambiental similar para os três componentes da diversidade betas analisados, sendo que foram selecionados preditores ambientais similares como mais explicativos para a variação na diversidade beta taxonômica e funcional e filogenética.

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De 33 comunidades avaliadas, 18 apresentam uma clara estrutura filogenética (agrupamento filogenético) e 12 apresentam agregação funcional.

A diversidade de atributos dos girinos é significantemente concentrada em poucos nós e próximos da raiz da filogenia, demostrando que girinos apresentam conservação filogenética de atributos na região estudada.

Uma significante parte da variação na estrutura filogenética das comunidades é explicada por seis variáveis ambientais selecionadas aqui (presença de potenciais predadores (peixes), condutividade da água, diversidade da estrutura de vegetação externa e interna, cobertura de dossel e oxigênio dissolvido). Já para a estrutura funcional, foram selecionados a diversidade da estrutura de vegetação externa, cobertura de dossel, área, oxigênio dissolvido e a presença de potenciais predadores (peixes). Todas as variáveis selecionadas são reconhecidamente importantes para o desenvolvimento, sobrevivência e consequentemente a ocorrência de girinos de anuros em poças, o que indica uma forte influencia ambiental sobre a estrutura das comunidades.

Vale apontar que os preditores foram similares em relação à estrutura filogenética e funcional, demostrando uma clara influencia de filtros ambientais sobre a montagem das comunidades refletindo tanto na estrutura funcional quanto filogenética. Essa influencia também foi encontrada embora menos importante para a variação espacial entre as comunidades, como evidencia o primeiro capitulo.

Assim, esses resultados evidenciam o significativo papel dos filtros ambientais sobre as comunidades de anuros, demostrando estar agindo muito mais sobre comunidades

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locais do que sobre a variação espacial da diversidade, levando a um padrão claro de estrutura funcional filogenética agregada em muitas comunidades.

Entretanto, acima de tudo, esses resultados demonstram o expressivo papel de filtros espaciais, o processo mais importante para a variação espacial da diversidade, limitando a dispersão de muitas especeis de anfíbios entre as comunidades de anuros das planícies costeiras do estado de São Paulo, sudeste do Brasil.