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Diversidade funcional em comunidades de girinos

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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, Área de Concentração – Ecologia e Comportamento, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista “Júlio de Mesquita Filho”, Campus São José do Rio Preto.

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RESUMO

Ecólogos estão cada vez mais interessados em entender o papel da variação das características fenotípicas na formação das comunidades e coexistência de espécies. A abordagem funcional permite uma melhor compreensão da distribuição da biodiversidade ao longo de diferentes tipos de habitat e gradientes ambientais. Os objetivos deste estudo foram: i) investigar o efeito do tipo de habitat (lêntico vs lótico) e de diferentes gradientes ambientais (cobertura de dossel, profundidade, área, quantidade de vegetação e volume) na diversidade funcional intraespecífica em comunidades de girinos na Mata Atlântica; e ii) quantificar a variação intra e interespecífica dos atributos fenotípicos em girinos de poças na Amazônia e na Mata Atlântica, e a influência da variabilidade fenotípica na formação de comunidades de girinos. Detectamos que a posição do espaço funcional diferiu nas comunidades de habitats lênticos e lóticos. Em habitats lênticos é possível encontrar girinos com diferentes atributos morfológicos, enquanto os girinos de habitats lóticos apresentaram morfologia especializada, como corpo deprimido, focinho curto, olhos pequenos, musculatura caudal espessa e nadadeiras dorsal e ventral baixas. Além disso, tanto nos habitats lênticos como nos lóticos, os girinos apresentaram diferentes atributos funcionais ao longo do gradiente de cobertura de dossel, indicando sua ação como filtro ambiental. Detectamos ainda que existe variação intraespecífica em girinos da Amazônia e da Mata Atlântica. A variabilidade intraespecífica foi relacionada com a altura da nadadeira dorsal e compressão da cauda, indicando diferenças na habilidade de natação entre as espécies. Detectamos também um forte efeito de filtros externos na montagem de comunidades de girinos em relação à largura da musculatura caudal nos indivíduos, e também ação de filtros internos em todos os atributos, exceto

os que variaram entre os indivíduos. Nossos resultados fornecem novas perspectivas para a compreensão da variação de atributos funcionais ao longo de diferentes ecossistemas aquáticos e gradientes ambientais.

Palavras-Chave: Anuros, Amazônia, atributos funcionais, coexistência de espécies, Mata Atlântica, montagem de comunidades

ABSTRACT

Ecologists are increasingly interested to understand the role of phenotypic trait variability on community assembly and species coexistence theories. The functional approach provides good insights about the biodiversity distribution along different types of habitat and environmental gradients. The aims of this study were i) to investigate the effect of aquatic habitat's type (lentic vs. lotic) and different environmental gradients (canopy cover, water depth, area and amount of aquatic vegetation) on intraspecific functional diversity of tadpoles assemblages from Atlantic Forest; ii) to quantify the intra and interspecific components of tadpoles trait variability from Amazon and Atlantic Forests, and also, to investigate the role of trait variability on tadpoles assembly community. We detected that the functional space position differed between lentic and lotic habitats. In lentic habitat is possible to find tadpoles with different morphological trait, whereas in lotic habitats, tadpoles present specialized morphology, as depressed body, short snout, smaller eyes, thicker tail, and lower dorsal and ventral fins. In addition, independent of the habitat type, tadpoles shown different functional traits along canopy cover gradient, which functions as an environmental filter to tadpoles' traits. We detected that besides the interspecific variability, there is a not negligible intraspecific variability in tadpoles from Amazon and Atlantic Forests. The intraspecific variability was mainly related to height of the dorsal fin and tail compression, indicating differences in swimming ability among species. We also found, a strong external filtering effect on tadpoles assembly related to width muscle tail on individuals, and also the action of internal filter all the others traits, excepted those that varied among individuals. Our results provide new perspectives for the understanding how the functional traits vary among different freshwater ecosystem and environmental gradients.

Key-words: Anura, Amazon and Atlantic Forests, assembly community, functional traits, species coexistence, trait variability

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INTRODUÇÃO GERAL

Ecólogos estão cada vez mais interessados em compreender o papel da variação das características fenotípicas na formação das comunidades e coexistência de espécies. A formação e manutenção das comunidades ecológicas, definidas como conjunto de organismos encontrados em um mesmo espaço e tempo, se dá pela chegada sequencial de potenciais colonizadores a partir de um banco regional de espécies (Ricklefs 1987, HilleRisLambers et al. 2012, Kraft et al. 2015). A ação de diferentes filtros ecológicos, constituídos por fatores abióticos e bióticos, desde a chegada até a persistência das espécies na comunidade local, seleciona as espécies de acordo com os seus atributos funcionais (Keddy 1992, Weiher & Keddy 1995, Weiher et al. 2011). Atributo funcional é qualquer característica fenotípica mensurável nos indivíduos (e.g. morfológica, comportamental, fisiológica) que afete, de maneira direta ou indireta, seu desempenho em crescer, reproduzir e sobreviver (McGill et al. 2006, Violle et al. 2007). Os filtros ecológicos podem ser distinguidos de acordo com a escala espacial em que atuam (Weiher et al. 2011, Violle et al. 2012). Em escalas espaciais amplas, filtros externos à comunidade, como o tipo de clima, solo, relevo, presença e ação de predadores generalistas, triam as espécies capazes de chegar na comunidade local a partir do banco regional de espécies (Ricklefs 1987, Violle et al. 2012). Já em escalas mais restritas, a interação entre os organismos (e.g. processos dependentes de densidade) e as características ambientais internas (e.g. heterogeneidade de habitat e microhabitat) atuam como filtros internos, regulando a persistência das espécies na comunidade local (Violle et al. 2012).

Uma das questões mais intrigantes em ecologia é a coexistência de um grande número de espécies em uma comunidade local, visto que muitas espécies utilizam os mesmos recursos e desempenham o mesmo papel ecológico em um contexto onde os recursos são na maioria das vezes limitados. Tradicionalmente, as teorias de coexistência e formação das comunidades consideram apenas a diferença média nas características fenotípicas entre as espécies para explicar a manutenção e padrões de diversidade (Violle et al. 2012). Entretanto, para melhor compreensão destas questões é necessário

investigar como os indivíduos de uma população interagem uns com os outros (interação intraespecífica) e com populações de diferentes espécies (interação interespecífica; Jung et al. 2010, Albert et al. 2010, Violle et al. 2012, Hart et al. 2016, Turcotte & Levine 2016). Trabalhos recentes demonstram que, além da variação interespecífica, grande parte da variação nos atributos também ocorre dentro das espécies (e.g. Cianciaruso et al. 2009, Albert et al. 2010, Jung et al. 2010, Bolnick et al. 2011, Siefert 2012), devido a mutações genéticas e plasticidade fenotípica.

A coexistência de espécies em uma comunidade local é dada pela interação de dois mecanismos gerados a partir de diferenças nos valores de atributos entre as espécies: diferenciação de nicho (*stabilizing niche difference*) e diferença na habilidade competitiva (*fitness difference*; Mayfield & Levine 2010, Turcotte & Levine 2016). De acordo com Chesson (2000), a diferenciação de nicho inclui diferenças nos valores de atributos entre as espécies que causam limitações às próprias espécies mais do que a seus competidores. Consequentemente, a competição intraespecífica se torna mais intensa do que a competição interespecífica (Mayfield & Levine 2010, Turcotte & Levine 2016), fazendo com que as espécies se mantenham em baixas densidades populacionais. A diferenciação de nicho pode ser exemplificada por diferenças entre as espécies no uso dos recursos que limitam o crescimento populacional, diferenças na interação com consumidores especialistas ou patógenos, ou ainda, diferenças no uso do espaço ambiental (Turcotte & Levine, 2016). Entretanto, a diferenciação de nicho não garante a coexistência estável. Os benefícios que as espécies obtêm com a baixa densidade devem ser suficientemente fortes para superar suas diferenças na habilidade competitiva. Diferenças no desempenho entre as espécies (*fitness difference*) refletem vantagens e desvantagens que as espécies têm uma em relação às outras. Como por exemplo, a capacidade de uma espécie se reproduzir quando os recursos são limitados e a outra não. Ou ainda, diferenças na tolerância de consumidores generalistas ou mesmo habilidade de esgotar um recurso limitado que é compartilhado. Entretanto, na ausência de diferença de nicho a diferença de *fitness* leva à exclusão competitiva (Mayfield & Levine 2010, Turcotte & Levine 2016). Portanto, a coexistência entre as espécies surge quando há diferenças sutis de nicho maiores que as diferenças na habilidade competitiva,

ou quando há fortes diferenças de nicho superiores a diferenças na habilidade competitiva (Chesson 2000, Mayfield & Levine 2010, Turcotte & Levine 2016).

Comunidades de anuros em fase larval (girinos) são excelentes sistemas para compreender a influência relativa da variabilidade intra e interespecífica na formação das comunidades e coexistência de espécies, devido à i) influência das interações bióticas e variáveis ambientais na distribuição espacial e desempenho das espécies, ii) a sua grande plasticidade fenotípica e iii) importante papel ecossistêmico. A fase larval dos anuros, em sua grande maioria, ocorre limitada a diferentes tipos de corpos d'água (McDiarmid & Altig 2010) e, devido a grande variedade de modos reprodutivos (Haddad & Prado 2005), os girinos podem ser encontrados em diferentes tipos de habitats aquáticos. Habitats lênticos, como poças, brejos e açudes, e habitats lóticos como riachos, rios e igarapés, são importantes ecossistemas aquáticos utilizados para reprodução dos anuros. Durante esta fase da vida, os girinos sofrem diferentes pressões bióticas e abióticas. A competição intra e interespecífica (e.g. Faragher & Jaeger 1998, Grampurohit et al. 2004) e a predação (Azevedo-Ramos et al. 1999, Barnett & Richardson 2002, Both et al. 2009) são forças bióticas que exercem fortes pressões nas comunidades de girinos. Além disso, fatores estruturais do habitat e físicos e químicos da água influenciam o desenvolvimento e sobrevivência dos girinos como, por exemplo, a duração dos corpos d'água (e.g. Wellborn et al. 1996, Babbitt & Tanner 2000, Sonodgrass et al. 2000, Babbitt et al. 2003, Babbitt 2005), a quantidade de vegetação, a condutividade da água (e.g. Both et al. 2009, Browne et al. 2009), a profundidade (e.g. Barreto & Moreira 1996, Browne et al. 2009) e o grau de cobertura de dossel (e.g. Van Buskirk 2011).

Os girinos exibem uma grande diversidade morfológica, desde girinos com morfologia generalizada (corpo oval, musculatura caudal larga e nadadeiras altas; Wells 2010), até girinos altamente especializados como girinos semiterrestres que possuem corpo achatado dorsoventralmente, olhos grandes e nadadeiras ausentes (Altig & Johnston 1989, McDiarmid & Altig 2010), Wells 2010). Grande parte desta variação envolve diferenças no formato do corpo, tamanho e formato das nadadeiras e morfologia do disco oral (Altig & Johnston 1989, McDiarmid & Altig 2010), que irão refletir a forma como as espécies utilizam os recursos disponíveis (e.g. comportamento de forrageamento para alimentação e posição na coluna d'água; Wells 2010). Os girinos exibem grande

plasticidade fenotípica (expressão de diferentes fenótipos de acordo com as condições ambientais, *sensu* Bradshaw 1965) como, por exemplo, diferenças no tempo de desenvolvimento, tamanho na metamorfose e aspectos fisiológicos, morfológicos e comportamentais, tanto em resposta às características físicas do ambiente (Eterovick & Barata 2006, Eterovick et al. 2010), como à presença de predadores e competidores (Releya 2005, Michel 2012). Os girinos possuem importante relevância na execução de processos ecossistêmicos em habitats aquáticos, como alterações na dinâmica de matéria orgânica por meio da remoção dos sedimentos, e na produtividade primária, alterando a composição e abundância de produtores primários pelo consumo de algas (Whiles et al. 2006, Hocking & Babbitt 2014).

As florestas tropicais abrigam grande diversidade de anuros, sendo encontradas em diferentes continentes, entre as latitudes 0° a 27° nos hemisférios norte e sul. Na América do Sul, as florestas Amazônica e Atlântica são importantes *hotspots* de biodiversidade (Myers et al. 2000, Jenkins et al. 2013) e ambas se encontram altamente ameaçadas devido à elevada e rápida taxa de desmatamento. Mesmo nessas florestas úmidas, habitats lânticos e lóticos ainda são os principais ecossistemas aquáticos utilizados pelos anuros para reprodução (Duellman & Trueb 1986) devido ao modo reprodutivo ancestral (com ovos e girinos aquáticos) estar presente na maioria das espécies (Gomez-Mestre et al. 2012). Para melhor compreensão da relação dos traços funcionais dos girinos com os processos de montagem e manutenção das comunidades, organizamos as questões abordadas neste estudo em dois temas principais, correspondentes aos capítulos da Tese. No primeiro investigamos o efeito do tipo de habitat (lântico vs lótico) e de diferentes gradientes ambientais (cobertura de dossel, profundidade, área e quantidade de vegetação) na diversidade funcional intraespecífica em comunidades de girinos na Mata Atlântica. No segundo capítulo, quantificamos os componentes intra e interespecíficos na variabilidade dos atributos fenotípicos dos girinos da Amazônia e Mata Atlântica, investigando o papel da variação intraespecífica na formação de comunidades de girinos.

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CAPÍTULO 1

Environmental filtering and Neotropical tadpoles functional
traits distribution *

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Environmental filtering and Neotropical tadpoles functional traits distribution

Neotropical tadpoles functional traits distribution

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Keywords: Anura, canopy cover, functional diversity, lentic, lotic

Summary

1. Trait-based approach provides insights into the mechanisms driving community organization and ecosystem functioning. Anurans are differentially distributed in lentic and lotic aquatic habitats. The structural differences between these habitats influence the composition, species richness, and abundance of anuran larvae. However, the functional diversity patterns in lentic and lotic tadpole assemblages are still unclear.
2. In this study, we investigated the effect of aquatic habitat's type on functional diversity of tadpole assemblages. Complementarily, we explored if there is variation in tadpoles functional traits along different environmental gradients as canopy cover, depth, surface area, and amount of aquatic vegetation. We predict that due to the gradual microhabitat change related to depth and aquatic vegetation availability in lentic habitats, tadpoles with different phenotypes will coexist. On the other hand, the running water which produce discontinuous microhabitat distribution acts as an environmental filter selecting tadpoles with morphological specialization related to the swimming ability leading the coexistence of tadpoles with similar phenotypes.
3. We analyzed seven morphological traits in 376 tadpoles from 22 species of 33 lentic habitats, and 68 tadpoles from 10 species in 10 lotic habitats in Atlantic Forest, Brazil. We used functional metrics based on multidimensional space to calculate functional richness, functional evenness, and the functional space position. The functional diversity in lentic and lotic habitats were compared, and to verify if the functional space position of each community varies along a canopy cover gradient we employed Linear Mixed Effect Models (LMM).
4. Despite the functional richness and functional evenness did not differ between lentic and lotic habitats, our results show that the functional space position differed between these two freshwater ecosystems. According to our prediction, in lentic habitats it is possible to find tadpoles with different morphological traits. In lotic habitats tadpoles present specialized morphology, as depressed body, short snout, smaller eyes, thicker tail and lower dorsal and ventral fins. Additionally, independent of the habitat type, tadpoles shown different functional traits along canopy cover gradient, which functions as an environmental filter to tadpoles' traits.
5. Our results present new perspectives for the understanding of how the functional traits vary among different aquatic habitats and environment gradients. The running water in lotic habitats and canopy cover act as environmental filters, selecting tadpoles with morphological specialization.

Keywords: Anura, canopy cover, functional diversity, lentic, lotic

Introduction

The importance of the process driving the biodiversity distribution in different types of habitat is crucial in the actual period of high loss of biodiversity (Barnosky *et al.*, 2011). In the last years, several studies have found that the trait-based approaches provides good insights on the relationship between biological diversity and ecosystem functioning (e.g., Tilman *et al.*, 1997; McGill *et al.*, 2006). In the functional diversity framework, the individuals and species are differentiated by morphological, physiological or behavioral characteristics, which indirectly impact their fitness via effects on growth, reproduction and survival (Violle *et al.*, 2007). Recent studies (e.g. Cianciaruso *et al.*, 2009; Jung *et al.*, 2010; Bolnick *et al.*, 2011) have highlighted the importance of intraspecific variability for the species coexistence and the dynamics of communities (Albert *et al.*, 2010). Intraspecific trait variability due to phenotypic plasticity or genetic diversity, determines the species abilities to cope with changes in environmental conditions and the interactions with others species (Jung *et al.*, 2010). By investigating the functional variation among coexisting species, insights on ecological processes of community assembly rules can be found (Kraft, Godoy & Levine, 2015a). In this context, functional traits approaches can be useful to study the role of environmental filtering in shaping community composition (Kraft *et al.*, 2015b).

Anuran larvae gather interesting characteristics for to understand the relationship between environmental gradients and functional traits distribution. First of all, they are differently distributed in several types of aquatic habitats, from small and highly ephemeral habitats as rainwater stored in bromeliads to large and permanent lentic and lotic habitats (Altig & McDiarmid, 1999). Not surprisingly, tadpoles exhibit a wide range of morphological variation related to differences in evolutionary history (Eterovick & Fernandes, 2001; Van Buskirk, 2009) and ecological aspects (Heyer, 1973; Hoff *et al.*, 1999; Strauß *et al.*, 2010; 2013). Large part of tadpoles morphological variation involves differences in the overall body shape, the size and shape of the tail fin, and in the morphology of the oral disc (Altig & McDiarmid, 1999; Wells, 2010). Finally, tadpoles have high functional relevance to freshwater ecosystems. Tadpole assemblages alter the patterns of primary production by changing algae species

abundance and composition, and also, by altering organic matter dynamics through reduction of sediment accumulation (Whiles *et al.*, 2006; Hocking & Babbitt, 2014).

Anuran larvae are typical and common components of two contrasted freshwater ecosystems: lentic and lotic habitats. Lentic habitats are closed systems with still water, which are important reservoirs of nutrients and other materials (Dodds & Whiles, 2010). The lentic habitat can be divided in different zones (littoral, pelagic, and deep water zones) according to the depth variability and availability of light (Dodds & Whiles, 2010). Lotic habitats are characterized by different hydraulic characteristics inside a lotic channel, ranging from areas of fast flow, such as riffles, to slow flow, such as runs and pools (Allan & Castillo, 2007). They are dynamic systems, with seasonal or daily periods of high and low flows, depending on climate, topography, geology, land cover, and site position (Poff & Zimmerman, 2010). Such variability in flow regime affects several environmental conditions, populational demography, and assemblages diversity (Dodds & Whiles, 2010; Poff & Zimmerman, 2010). In lentic habitats, the microhabitat heterogeneity shows no clear boundaries, with a gradual transition between different microhabitats. Moreover, depth, light intensity, temperature, and amount of oxygen and nutrients vary gradually in lentic habitats (Lampert & Sommer, 1997; Dodds & Whiles, 2010). On the other hand, in lotic habitats, beside the microhabitat with well delimited boundaries, the water current represents a selective factor to the species distribution inside habitat (Lampert & Sommer, 1997; Dodds & Whiles, 2010).

Beside the structural and dynamic differences between lentic and lotic habitats, in both freshwater ecosystems, the degree of canopy cover control the energy input to aquatic habitat. The primary productivity is often considered to be a primary determinant in species composition, coexistence, and diversity (Chase, 2003). With the increase of canopy cover degree, closed canopy areas have low solar incidence, water temperature, dissolved oxygen, consequently low primary productivity and low quality food resource (Werner & Glennemeier, 1999; Skelly, Freidenburg & Kiesecker, 2002; Schiesari, 2006). The difference in spatial and temporal heterogeneity in environmental conditions of lotic and lentic habitats, make them good candidate to investigate the effect of environmental filtering on functional diversity in freshwater ecosystem.

Here, we investigated the effect of aquatic habitat's type on functional diversity of tadpole assemblages at the Atlantic Forest in Brazil. Complementarily, we explored if the features of aquatic habitats (canopy cover, aquatic vegetation, volume, area, depth) affect the functional diversity distribution. We predict that in lentic habitats, due to the gradual microhabitat change in water depth and aquatic vegetation availability, tadpoles with different phenotypes will coexist. On the other hand, in lotic habitat, the running water acts as an environmental filter, selecting tadpoles with morphological specialization related to the swimming ability leading the coexistence of tadpoles with similar phenotypes.

Methods

Study area

The Atlantic Rain Forest lowlands are located from 5 m to 50 m of altitude from 16° to 24° South (IBGE, 2012), occurring at the coastal plains with vegetation characterized woody trees of medium and large sizes, lianas and epiphytes (IBGE, 2012). Aquatic habitats were sampled in four different localities: Bertioga, Iguape, Itanhaém, and Ubatuba. Bertioga, Iguape and Itanhaém cities have tropical climate, without dry season (Af Köppen Geiser classification, Alvares *et al.*, 2013). The climate in Ubatuba is humid subtropical, with influence of the oceanic climate, without dry season and with hot summer (Cfa Köppen Geiser classification, Alvares *et al.*, 2013). Both climates are characterized by high temperatures (average: Af = 21.5 °C; Cfa = 20.8) and high rainfall well distributed throughout the year (cumulative annual rainfall: Af = 2309 mm; Cfa = 2243 mm; Figure S1; Alvares *et al.* 2013).

Data acquisition

We used a subset database from Atlantic Forest obtained by the Project “Tadpoles from Atlantic Forest, Amazon, Pantanal, Cerrado, and transition zones: morphological description, spatial distribution and diversity patterns”

(SISBIOTA, Processes: CNPq 563075/2010-4 and FAPESP 2010/52321-7) from 2011 to 2013. A standardized protocol was used for tadpoles sampling and characterization of aquatic habitats in different locations. Tadpoles were sampled using a hand dip-net (32 cm diameter) with a 3 mm² mesh. Dip-net surveys were made throughout the total area of lentic habitats (Rossa-Feres & Jim, 1996; Skelly & Richardson, 2010) and along 100 m transect in lotic habitats, until the entire area may have been sampled or until the maximum time of one hour in each habitat. For each aquatic habitat, we compiled the following environmental variables: percentage of canopy cover, surface area (m²), volume (m³), maximum depth (cm), and amount of aquatic vegetation (Table S1). Canopy cover was estimated with a concave spherical densiometer (Forest densiometer model C; Lemmon, 1956) at four points located in each quarter of habitat, being considered the mean for each habitat. Surface area was calculated multiplied the greater width by greater length, and volume was calculated applying the formula: volume = surface area x average depth (Almeida *et al.*, 2015). The maximum depth was measured in the center of each habitat. Amount of aquatic vegetation was visually estimated considering three classes of vegetation cover: 1 for 0 to 20%, 2 for 21 to 60%, and 3 to 61 to 100% of water body. For lotic habitats, the volume, surface area, canopy cover, and depth was estimated each 25 m, and being considered the mean value along 100 m transect

We analyzed all tadpole assemblages with more than three individuals sampled between the developmental stages 33 and 37 (Gosner, 1960), which are the adequate stages to morphological analyzes. The dataset was constituted by tadpole assemblages from 33 lentic and 10 lotic habitats, in Lowland Ombrophilous Dense Forest, in southeast Brazil (Figure 1; Table S1). The tadpoles are deposited in DZSJRP - Amphibia Tadpoles Collection of Department of Zoology and Botany, Universidade Estadual Paulista (UNESP), São José do Rio Preto, Brazil.

Functional traits

Eight functional traits were obtained from 10 morphological features (Table 1) that are known to be related to resource use, such as feeding behavior (Altig & Johnston, 1989; Harris, 1999), position in water column (Altig & Johnston, 1989; Alford, 1999; Hoff *et al.*, 1999) and tadpoles hydrodynamics (Altig & McDiarmid, 1999). The traits were measured on 376 tadpoles (22 species) from lentic habitats and 68 tadpoles (10 species) from lotic aquatic habitats (Table 2). All morphological features were measured in millimeters under a stereoscopic microscope with ocular micrometer (Leica MZ75) and later converted into indices for the relative size (Table 1).

Statistical analyses

Taxonomic diversity

To investigate if lentic and lotic habitats have different species composition, we determined the amount of shared species using the incidence-based Jaccard adjusted estimator (Chao, Chazdon & Shen, 2005). Incidence-based Jaccard considers *unseen* shared species into account to reduce the sample-size bias and large proportion of rare species (Chao *et al.*, 2005). We used a bootstrapping procedure to estimate the total relative incidences of the shared species in the one assemblage (lentic habitat) and the total relative incidences of the shared species in the other assemblage (lotic habitat). The randomization process was carried out 99 times.

Functional metrics

To reduce dimensionality and correlations among the functional traits, we performed a principal component analysis (PCA). For this, first we standardized the traits values for all functional traits have the same weight in functional diversity estimation (Villéger *et al.*, 2008). We selected the first two principal component axes to calculate different functional metrics based on multidimensional space: two metrics of functional richness (Villéger *et al.*, 2008;

Fontana, Petchey & Pomati, 2016), two metrics of functional evenness (Villéger *et al.*, 2008; Fontana *et al.*, 2016), and the functional space position.

Functional richness (FRic) represents the changes in trait values in the functional space occupied by the community (Villéger *et al.*, 2008). FRic quantify the volume (or area in two dimensions) inside the convex hull enclosing all the individuals from each community (Cornwell, Schvilk & Ackerly, 2006; Villéger *et al.*, 2008), considering the most extreme trait value (Figure 2a). Here, the convex hull represents the perimeter of the polygon. The FRic values were standardized by the global hull volume (the volume occupied by all individuals), ranging from 0 to 1 (Villéger *et al.*, 2008). We calculated another functional richness metric, the TOP (Trait Onion Peeling), which represents the sum of all successive convex hull areas touching all individual (points) within a multidimensional functional space (Fontana *et al.*, 2016; Figure 2a). For both metrics (FRic and TOP) assemblages containing individuals exhibiting a low range of trait values have low functional richness and assemblages with individuals having different combinations of traits have a high functional richness. However, whereas the FRic considers the variation between individuals located on the extreme, the TOP include the trait values inside the perimeter of the polygon.

Functional evenness describes the regularity among individuals of a community across a functional trait gradient, showing how functional space is filled (Villéger *et al.*, 2008). To calculate functional evenness index (FEve), a minimum spanning tree is used to link all the individuals in the multidimensional functional space with minimum sum of branch lengths (Villéger *et al.*, 2008; Figure 2b). We also employed another functional metric adapted to individual-level trait evenness, the TED (Trait Even Distribution) that measures how evenly individuals are distributed within the multidimensional functional space. TED is calculated comparing the probability distributions of pairwise distance between individuals and between points of a perfectly even reference distribution (Fontana *et al.*, 2016).

The volume and regularity among the individuals on functional trait space can be similar between assemblages. However, the position of functional space can change. Because that, we analyzed the functional space position (FSP) of each tadpoles community, using a simplified form of functional metrics that

measure the centroid of the community in trait space, such as, functional divergence (FDiv; Villéger *et al.*, 2008) and dispersion (FDis; Laliberté & Legendre, 2010). The functional space position (FSP) represents the traits values distribution among the individuals of community. This index summarize shifts in mean trait values among assemblages due to environmental filtering (Ricota & Moretti, 2011) and allow to investigate which tadpoles traits are filtered across different aquatic habitat. To this end, we calculated the centroid value of the functional space at the perimeter of the convex hull relative to first (PC1) and second component (PC2) obtained from principal component analysis (Figure 2c). These indices will be referred by FSP1 and FSP2 hereafter. The functional richness (FRic) and evenness (FEve) were calculated in R 3.2.3 (R Core Team, 2016), using FD package (Laliberté *et al.*, 2014). The TOP (Trait Onion Peeling) and TED (Trait Even Distribution) were calculated using the function described by Fontana, Petchey & Pomati (2015). The functional space position (FSP1 and FSP2) was measured using the apply function in R.

Because functional richness increases with the number of individuals in each community, we used a null model approach to remove any trivial effects of number of individuals (Mason *et al.*, 2013). We created 999 random species composition matrices where species richness per community was conserved, but the individuals identity was randomized. We then computed the ratio between the functional richness observed and the mean of the null values community. Although the functional evenness is independent of number of individuals, we decided to use the ratio between the observed and mean of random expected for both metrics, functional richness and evenness. Hereafter these indices will be referred by FRic.ratio and FEve.ratio.

Data analysis

Before applying any statistical analyses, data exploration following the protocol described in Zuur *et al.* (2010) was carried out. The presence of outliers in the response variables (each functional metrics) and continuous covariates were investigated with Cleveland dotplots (Zuur *et al.*, 2010).

Collinearity (relationships between covariates – predictors variables) was assessed with variance inflation factors (VIF). We calculated the VIFs and sequentially dropped the variables with highest VIFs until all variables had VIFs smaller than 3 (Zuur *et al.*, 2010). The data exploration indicated that the response variables FRic and TOP, and explanatory variables volume and area of freshwater habitats contained outliers. Therefore, we applied a logarithmic transformation in the explanatory and these variables are designed by log.FRic, log.TOP, log.volume, log.area. Nevertheless, VIF (variance inflation factors) values indicated the presence of collinearity and we decided not to include the log.volume (VIF = 3.35) in the following analysis. VIF values of all remaining covariates were smaller than 3. Graphic representation, as scatterplots and boxplots, were used to detect if there was a linear or non-linear relationship between each covariate and each response variable. During the data exploration we visually not found any relationship between the functional metrics (log.FRic, FRic.ratio, log.TOP, FEve, FEve.ratio, and TED) and environmental characteristics of the aquatic habitats. Therefore, we included just the functional space position (FSP1 and FSP2) to investigate the relationship between functional diversity and the environmental characteristics of aquatic habitats (second aim).

Finally, we analyzed the effect of aquatic habitat's type (explanatory variable – nominal with two levels) on functional diversity of tadpole assemblages (continuous response variable). Then, we investigated if there was a relationship between shifts in functional traits (functional space position) and the environmental characteristics of aquatic habitats. For both analyses, we fitted a linear mixed effect models for nested data for each functional metric (Zuur *et al.*, 2009). The data were considered nested because multiple observations (tadpole assemblages) were taken from the same locality. We thus included localities (Bertioga, Iguape, Itanhaém, and Ubatuba) as random effects to account for the non-independence of assemblages sampled within the same municipality.

To investigate which environmental variables best explained the functional diversity, for each response variable (FSP1 and FSP), we fitted a full model including canopy cover, depth, area (log), and amount of aquatic vegetation. To find the optimal set of covariates we used a top-down strategy

for model selection (Zuur *et al.*, 2009). Initially, the best random effect structures, with all fixed effects considered, were selected using the smallest AIC value. Models were fitted with lme function in the nlme package in R (Pinheiro *et al.*, 2016), using restricted maximum likelihood (REML). After finding the best random effect structures, the best combination of fixed effects was selected using maximum likelihood (ML) estimations and likelihood ratio test (LRT) to conduct a sequential backward elimination of nonsignificant terms ($p > 0.05$). LRT statistics for all variables dropped from models as well as outputs from final models are listed in Tables S1. Residuals were checked using diagnostic plots (Zuur *et al.*, 2009).

Results

We found that only tadpoles of five species, from 22 species of lentic and 10 species of lotic habitats, occurred in these two types of freshwater ecosystems. The compositional similarity between the habitat types was low (Incidence-based Jaccard = 0.33; s.e. $\pm$ 0.09). The total relative incidence of the shared species in lentic habitats was higher than in lotic habitats (Lentic: $U=0.911$, s.e.=0.20; Lotic: $V=0.35$; s.e.=0.13), indicating that the species composition of lentic habitats is more similar among themselves than those of tadpole assemblages in lotic habitats.

The first two principal component axes explained 53% of the trait variation. The first PCA axis ordered the tadpoles according to body compression index, length of snout, diameter of the eyes (Table 3). On the left portion of the PCA biplot are found tadpoles with depressed body, short snout and small eyes, and on the right, are found tadpoles with globular bodies, long snout and big eyes (Figure 3). The second PCA axis ordered tadpoles according to tail compression index, width of the tail, and height of the dorsal and ventral fins (Table 3). On the upper side of PCA biplot are found tadpoles with broader and thicker tail muscle, and lower dorsal and ventral fins, and on bottom tadpoles with compressed, narrower tail muscle, and higher dorsal and ventral fins (Figure 3).

Values of functional richness (log.FRic, FRic.ratio and log.TOP metrics) and functional evenness (FEve, FEve.ratio and TED) metrics did not differ between lentic and lotic habitats (Table 4). However, both functional space position, FSP1 and FSP2, differed between lentic and lotic assemblages (Table 5; FSP1 - Test F: $F_{1,38} = 4.37$; $p = 0.04$; Figure 4a; FSP2 - Test F: $F_{1,38} = 4.48$; $p = 0.03$; Figure 4b), evidencing that tadpoles traits values are differentially distributed among these freshwater systems. Tadpoles of lentic habitats exhibited globular body, longer snout, bigger eyes (right portion of the first PCA axis in Figure 3), and narrow, compressed and thinner tail with higher dorsal and ventral fins (top portion of the second PCA axis in Figure 3). Tadpoles of lotic habitats exhibited depressed body, short snout, smaller eyes (left portion of the first PCA axis in Figure 3), and broad and thicker tail and lower dorsal and ventral fins (down portion of the second PCA axis in Figure 3) occurred in lotic habitats.

Additionally, we detected an effect of environmental features on functional space position regardless of habitat type. The model that better explains the effect of environmental variables in functional diversity in tadpole assemblages was the canopy cover percentage in relationship to FSP1 ($df = 2$; $LRT = 15.43$; $p < 0.001$). See Table S2 for likelihood ratio test statistics for dropped variables of the full model (canopy cover, depth, area (log), and amount of aquatic vegetation) and the LME outputs for the optimal set of covariates in the final models. We added non-significant term canopy cover x habitat type in model to improve the model validation. The functional space position (FSP1) changes over the canopy cover gradient (Figure 5). Tadpoles with globular body, longer snout and bigger eyes occurred in aquatic habitats in open areas (right portion of the first PCA axis in Figure 3). With increasing of canopy cover, tadpoles exhibited depressed body, short snout and smaller eyes (left portion of the PCA axis in Figure 3).

Discussion

Lentic and lotic aquatic habitats have different anuran species composition, since only 15% of species occurred in both habitats. Anuran

species of lentic habitats are among the most well-recognized and extensively studied group around the world, including the Brazilian Atlantic Forest (e.g. Vasconcelos *et al.*, 2009; Both *et al.*, 2009; 2011; Prado *et al.*, 2014; Provete *et al.*, 2014). There is a great diversity of anuran species in lentic habitats, mainly of Bufonidae, Hylidae, Microhylidae, and Leptodactylidae families. In contrast to lentic, neotropical tadpole assemblages in lotic habitats houses lower anuran diversity (Inger & Voris, 1993; Eterovick & Fernandes, 2001; Eterovick, 2003). The spatial and temporal heterogeneity in environmental conditions encountered within these systems (Dodds & Whiles, 2010) seem to improve the difference in species composition between lotic and lentic habitat. Tadpoles in lotic habitat display morphological and behavior adaptations to live in a particular stream microhabitat (Gascon, 1991; Eterovick *et al.*, 2010). This is because the water current act as an environmental filtering (Lampert & Sommer, 1997) in lotic habitat act which, asides selecting anurans species adapted to reproduce and persist in this kind of habitat, hinders the displacement of tadpoles between microhabitats. Additionally, our results show that the species composition in lentic habitats is more similar among themselves than those of lotic habitats. There are evidences that, at a landscape scale distribution, the species composition of tadpole assemblages is essentially influenced by behavioral decisions of adults in response to environmental gradients (Provete *et al.*, 2014). The different structure and spatialization of lentic and lotic habitats can also influence the adult dispersion. The dispersion by adults is more frequent between ponds, whereas in lotic habits the adult dispersion seems to be easier along the margin in the same lotic habitat (Menin, Waldez & Lima, 2011) than between streams, which can explain the fact of lotic habitat has more different species composition.

While species composition differed, unlike our prediction, the range of trait values (functional richness metric) in tadpole assemblages and how evenly individuals are distributed within the multidimensional traits (functional evenness metric) did not differ between both freshwater ecosystems. Considering the total functional space for each one of habitat type, there was a considerable overlap in the set of functional traits among tadpoles from lentic and lotic habitats. It can be explained by the occurrence of tadpoles with generalized morphology in lotic habitats. Excepting *T. mesophaeus*, all the other four species found in both

habitats (*A. plastodiscus*, *S. tymbamirim*, *P. atlanticus*, and *H. semilineatus*) exhibit generalized morphology (Bokermann, 1963; Haddad & Sazima, 2004; Carvalho-e-Silva & Carvalho-e-Silva, 2005; Nunes, Kwet & Pombal, 2012). Tadpoles with generalized morphology, represented by oval body with broad muscular tail and wide tail fins (Wells, 2010), are found in different aquatic habitats. They are also adapted to feed on a variety of food (Wells, 2010). The occurrence of these species in lotic habitats can be explained by the variability in hydraulic characteristics inside a lotic channel (Allan & Castillo, 2007).

Tadpoles with generalized morphology are confined to quiet pools and backwater areas due to smallest flow water and higher food availability (Strauß *et al.*, 2013). Thus, the presence of tadpoles with generalized morphology in lentic and lotic habitats, drive the same pattern of functional richness and evenness in these two freshwater ecosystems.

However, the functional space position differed between lentic and lotic. The shift in functional space position indicates that tadpole traits values are differentially distributed among these freshwater systems. Despite some tadpoles with generalized morphology have been found in both freshwater ecosystem, tadpoles in lotic habitats presented lower morphological variation. The difference in traits distribution between lentic and lotic habitat can be related to the water flow (Lampert & Sommer, 1997), which acts as an environmental filtering selecting specific tadpole traits. Tadpoles of lotic habitats tend to have slightly thicker, more muscular tails and shorter tails fins than tadpoles of lentic habitats (Altig & McDiarmid, 1999; Wells, 2010). According to this, we found that tadpoles of lotic habitats presented depressed body, short snout, smaller eyes, thicker tail and lower dorsal and ventral fins. These traits represent adaptations to live in fast flowing streams (Altig & McDiarmid, 1999; Wells, 2010).

In opposite, our results showed that in lentic habitats it is possible to find tadpoles with different morphological traits specially of body and tail shapes, resulting in higher tadpoles trait variability in lentic than in lotic habitats. These findings disagree from Wells (2007), who argues that considering the variety of microhabitats in tropical streams, tadpole assemblages from lotic habitats will show greater interspecific morphological diversity than tadpoles from lentic habitats. In fact, there is a wide variety of microhabitats in lotic habitats, but the

dominant pressure in determining species composition seems to be the water current which selects species with adequate reproduction and development characteristics to live in streams. However, we cannot disregard the historical effect related to differences in regional pool from American and others continents. For instance, only 10% of the anuran species in Amazon Forest breed in lotic habitats (Gascon, 1991; Magnusson & Hero, 1991). In contrast, in other regions like Borneo and Madagascar there are a high proportion of anuran species breeding in lotic habitats (Heyer, 1973; Inger, Harold & Frogner, 1986; Parris & McCarthy, 1999; Strauß *et al.*, 2010; 2013). Thus, also the lower species richness may explain the lower morphological variation of tadpoles in Brazilian streams. These differences in species richness patterns probably are due to the topographical variation that influence the availability of lentic habitat in different regions (Strauß *et al.*, 2013), and also due to phylogenetic history, that determines the distribution of species with or without adequate traits to reproduce in lotic habitat in different continents (Zimmerman & Simberloff, 1996).

Another variable with important influence on tadpole traits distribution was found out of freshwater habitats. The canopy cover degree influenced the functional space position related to the first axes obtained from PCA. In open canopy aquatic habitats, tadpoles exhibited globular body, longer snout and bigger eyes, while in closed canopy cover tadpoles exhibited depressed body, shorter snout, and smaller eyes. Thus, tadpoles from lentic and lotic habitats in forest areas exhibited similar functional traits. This suggest, beside of the effect of habitat type, that canopy cover also acts as an environmental filter to tadpoles' traits. This results can be explained by effect of canopy cover on the quantity and quality of food availability (Schiesari, 2006). In closed habitats, both lentic and lotic ones, the primary productivity is lower than in open-canopy habitats, and the mainly resource available are detritus (Schiesari, 2006) and food attached to the substrate, as algae attached to rocks (Wells, 2010). The food availability for tadpoles in lotic habitat is concentrated in the bottom of pond, selecting benthic tadpoles. In opposite, aquatic habitat in open areas show high productivity levels and great abundance of algae along water column, allowing the occurrence of both benthic (globular body and longer snout) and nektonic tadpoles (big eyes; Wells, 2010).

Our results show that despite a large overlap, the tadpoles functional traits are influenced by the characteristics of aquatic habitats. The overlap in species composition and functional richness and evenness between the two types of habitats occurs because some microhabitats in lotic habitats are formed by quiet pools, resembling lentic habitats. Due to this, the range of traits values (functional richness) and how the functional space is filled by individuals (functional evenness) did not differ between lentic and lotic habitats. However, the functional space position, that represent the centroid position of the assemblage in functional space differed among the habitat type and across the canopy cover degree, indicating a joint action of running water in lotic habitats and canopy cover as environmental filters for tadpoles traits.

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Tables

Table 1: Eight functional traits measured in 376 tadpoles from 22 species of lentic habitat and 68 tadpoles from 10 species of lotic aquatic habitats, totalizing 444 tadpoles from 27 anurans species.

Abbreviation	Trait index description	Biological interpretation	Ecological function
BCI	Body compression index = body height / body width	Higher values indicate globular body, and lower values, depressed body	Nektonic tadpoles have globular body and they are more active swimmers. Benthic and nektonic tadpoles from family Microhylidae have depressed body. Tadpoles that live in flowing water have depressed body (Altig & Johnston 1989; Altig & McDiarmid 1999; Van Buskirk 2009)
TCI	Tail compression index = tail muscle height / tail muscle width	Higher values indicate compressed and thinner tail, and lower values, thicker tail	Variations in muscle tail reflect different position in the water column, swimming mechanics and styles. Thicker and stiff tail muscle is necessary for tadpoles living in water current, while pond-dwelling tadpoles have thinner and more flexible tail (Altig & McDiarmid, 1999)
RWT	Relative width of the tail = tail muscle width / body width	Higher values indicate broad tail muscle, and lower values, narrow tail muscle	Nektonic tadpoles have narrow tail muscle. Benthic tadpoles have broad tail muscle, facilitating they escape from active predators (Altig & McDiarmid 1999, Van Buskirk & Relyea 1998; Van Buskirk 2009)
HDF	Relative height of the dorsal fin = maximum dorsal fin height / body height	Higher values indicate higher fin, and lower values lower fin	Nektonic tadpoles have high dorsal fins which keep them in equilibrium and facilitates their displacement in the water column. Benthic tadpoles have low dorsal fins (Hoff & Wassersug 2000, Altig & Johnston 1989; Altig & McDiarmid 1999)
HVF	Relative height of the ventral fin = maximum ventral fin height / body height	Higher values indicate higher fin, and lower values lower fin	Nektonic tadpoles have high ventral fins which keep them in equilibrium and facilitates their displacement in the water column. Benthic tadpoles have low dorsal fins (Hoff & Wassersug 2000, Altig & Johnston 1989; Altig & McDiarmid 1999)
RLS	Relative length of snout = distance from eyes to snout / body length	Higher values indicate longer snout, and lower, shorter snout	The length of snout can facilitate the access to food in restricted places.
RDE	Relative diameter of the eyes = eye diameter / body length	Higher values indicate bigger eyes, and lower, smaller eyes	Nektonic tadpoles have larger eyes than benthic tadpoles. Fossorial tadpoles have very small eyes. (Altig & Johnston 1989; Altig & McDiarmid 1999)
RDN	Relative diameter of the nares = nares diameter / body length	Higher values indicate bigger nares, and lower, smaller nares	Variations in nares diameter is related to chemical perception of smells due to, in bigger nares, circulates larger volume of water (Altig & McDiarmid 1999)

Table 2: Anuran species analyzed from lentic and lotic habitats, sampled in Lowland Ombrophilous Dense Forest, in southeast Brazil.

Family	Species	Number of individuals analyzed	Habitat	
			Lentic	Lotic
Bufonidae	<i>Rhynella ornata</i>	24	X	
Cycloramphidae	<i>Cycloramphus boraceiensis</i>	5		X
	<i>Thoropa taophora</i>	12		X
	<i>Aplastodiscus eugenioi</i>	29	X	X
	<i>Dendropsophus berthalutzae</i>	7	X	
	<i>Dendropsophus elegans</i>	12	X	
	<i>Dendropsophus microps</i>	4	X	
	<i>Dendropsophus minutus</i>	9	X	
	<i>Dendropsophus weneri</i>	10	X	
	<i>Hypsiboas albomarginatus</i>	40	X	
	<i>Hypsiboas faber</i>	6	X	
Hylidae	<i>Hypsiboas semilineatus</i>	31	X	X
	<i>Itapotihyla langsdorffii</i>	8	X	
	<i>Scinax angrensis</i>	10		X
	<i>Scinax argyreornatus</i>	10	X	
	<i>Scinax hayii</i>	15	X	
	<i>Scinax littoralis</i>	1	X	
	<i>Scinax perereca</i>	7	X	
	<i>Scinax trapicheiroi</i>	20	X	
	<i>Scinax tymbamirim</i>	76	X	X
	<i>Trachycephalus mesophaeus</i>	21	X	X
Hylodidae	<i>Hylodes asper</i>	6		X
	<i>Hylodes phyllodes</i>	4		X
Leptodactylidae	<i>Leptodactylus latrans</i>	20	X	
	<i>Physalaemus atlanticus</i>	48	X	X
Microhylidae	<i>Chiasmocleis carvalhoi</i>	2	X	
	<i>Elachistocleis bicolor</i>	7	X	

Table 3: Loadings from Principal Components Analysis (PCA) of tadpoles functional traits. The values that contributed the most to the first and second axes are represented in bold (loadings <-0.4 or >0.4). The first and second axes explained, respectively, 32% and 21%, of the total tadpoles trait variation.

Functional traits	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Body compression index	0.497	-0.031	0.067	-0.175	0.514	-0.534	-0.339	0.231
Tail compression index	-0.126	-0.446	0.170	-0.612	0.370	0.493	-0.029	-0.026
Height of the dorsal fin	0.360	-0.417	-0.138	0.466	-0.012	0.383	0.055	0.557
Height of the ventral fin	0.380	-0.487	0.245	0.225	-0.055	-0.131	0.202	-0.668
Length of snout	0.447	0.040	-0.094	-0.379	-0.646	0.167	-0.446	-0.050
Diameter of the eyes	0.453	0.339	-0.127	-0.316	0.044	0.087	0.742	0.061
Diameter of the nares	0.023	-0.052	-0.889	0.032	0.259	0.085	-0.126	-0.341
Width of the tail	0.240	0.519	0.270	0.287	0.333	0.515	-0.275	-0.258

Table 4: Test F from Linear Mixed-Effect Model to investigate the effect of aquatic habitat's type on functional diversity of tadpoles assemblages. Response variables were: functional richness (logFRic, FRic.ratio and logTOP metrics) and functional evenness (FEve, FRic.ratio and TED). The predictor variable was habitat type (lentic and lotic).

Response variable	F-value	p-value
FRic	F-value _{1,38} = 1.29	p-value = 0.26
FRic.ratio	F-value _{1,38} = 0.07	p-value = 0.80
TOP	F-value _{1,38} = 1.79	p-value = 0.19
FEve	F-value _{1,38} = 0.86	p-value = 0.36
FEve.ratio	F-value _{1,38} = 1.05	p-value = 0.31
TED	F-value _{1,38} = 0.67	p-value = 0.42

Table 5: Results from Linear Mixed-Effects model fit by REML to investigate the effect of aquatic habitat's type (lentic and lotic) on functional space position (FSP1 and FSP2) of tadpoles assemblages.

Response variable	Explanatory terms	Estimate d Intercept	Estimate d Slope	Standard errors	t-value s	p-value s
FSP1	Habitat	0.23	-0.84	0.40	-2.09	0.04
FSP2	Habitat	-0.05	0.87	0.39	2.19	0.03

Table S1: Environmental features each habitat sampled Lowland Ombrophilous Dense Forest, in southeast Brazil.

Site	Habitat type	Localities	Latitude	Longitude	Depth (m)	Amount of Vegetation	Canopy cover (%)	Volume (m ³)	Area (m ²)
MAPI10	lentic	Ubatuba	-23.3583	-44.8172	0.14	2	86.1	7.03	75.43
MAPI09	lentic	Ubatuba	-23.3633	-44.8214	0.56	2	95.3	21.14	56.64
MAPI11	lentic	Ubatuba	-23.3769	-44.8185	0.86	1	91.9	30.06	52.44
MAPI04	lentic	Ubatuba	-23.3556	-44.8158	0.18	1	0	0.18	1.47
MAITA01	lentic	Itanhaém	-24.1986	-46.9394	0.27	3	0	30.55	169.74
MABER09	lentic	Bertioga	-23.762	-45.9163	1.6	3	33	372.33	350
MAPI05	lentic	Ubatuba	-23.3459	-44.8483	0.3	1	74.15	12.44	62.19
MAJUR04	lentic	Iguape	-24.5338	-47.2039	0.95	3	0	722	1140
MABER10	lentic	Bertioga	-23.7265	-45.7528	0.4	3	0	266.67	1000
MAPI02	lentic	Ubatuba	-23.3591	-44.8336	0.46	2	8.4	1697.22	5534.4
MAUBA09	lentic	Ubatuba	-23.3564	-44.8536	0.25	3	82	133.33	800
MAPI14	lentic	Ubatuba	-23.3588	-44.8335	0.4	2	0	32.45	121.69
MAJUR02	lentic	Iguape	-24.4621	-47.1104	0.8	3	74	240.8	451.55
MAUBA06	lentic	Ubatuba	-23.3563	-44.8266	0.6	3	72	106.8	267
MABER06	lentic	Bertioga	-23.7355	-45.9312	1.2	3	69	192	240
MAUBA08	lentic	Ubatuba	-23.3644	-44.8324	0.5	3	0	1333	4000
MABER12	lentic	Bertioga	-23.7362	-45.7471	0.6	3	0	600	1500
MAUBA03	lentic	Ubatuba	-23.3602	-44.8498	1.3	3	58	1009.29	1164.6
MABER02	lentic	Bertioga	-23.7433	-45.8655	1.5	3	0	8961.2	8961.2
MABER11	lentic	Bertioga	-23.7336	-45.7476	1.1	3	78	366.66	500
MAITA03	lentic	Itanhaém	-24.2249	-46.8944	1.5	3	0	4129.99	4130
MABER04	lentic	Bertioga	-23.7438	-45.7634	1.1	3	54	117.33	160

Table S1: Continuation. Environmental features each habitat sampled Lowland Ombrophilous Dense Forest, in southeast Brazil.

Site	Habitat type	Localities	Latitude	Longitude	Depth (m)	Amount of Vegetation	Canopy cover (%)	Volume (m ³)	Area (m ²)
MAPI07	lentic	Ubatuba	-23.3571	-44.8508	0.3	1	74.15	1505	2.82
MAJUR06	lentic	Iguape	-24.5728	-47.2478	0.65	3	43	490.33	1131.52
MAJUR01	lentic	Iguape	-24.4444	-47.0903	1	3	65	1367.66	2051.5
MAUBA04	lentic	Ubatuba	-23.3589	-44.8507	0.6	3	69	36.79	91.98
MAITA04	lentic	Itanhaém	-24.2341	-46.9264	0.45	3	81	22.5	75
MAITA05	lentic	Itanhaém	-24.2407	-46.9144	0.25	3	0	61.54	382.2
MABER07	lentic	Bertioga	-23.7544	-45.9265	1.1	3	64	187.66	256
MAITA08	lentic	Itanhaém	-24.2326	-46.9265	1.6	3	70	125.04	117.26
MAITA07	lentic	Itanhaém	-24.2463	-46.931	2	3	0	4239.77	3120
MAUBA05	lentic	Ubatuba	-23.3593	-44.8327	0.1	3	0	3.93	58.5
MAITA02	lentic	Itanhaém	-24.2173	-46.8946	0.4	3	0	1560	5850
MAITA11	lotic	Itanhaém	-24.2396	-46.928	1.4	2	70	457.31	490
MAPI15	lotic	Ubatuba	-23.3541	-44.7669	0.82	1	84.9	408.35	747
MAPI17	lotic	Ubatuba	-23.3612	-44.7711	0.77	1	91.7	289.51	564
MAPI18	lotic	Ubatuba	-23.3594	-44.7843	0.19	1	91.7	25.84	204
MAPI19	lotic	Ubatuba	-23.3512	-44.8136	0.89	1	90.5	468.13	789
MAPI20	lotic	Ubatuba	-23.3641	-44.8266	0.5	1	91.2	196.33	589
MAPI22	lotic	Ubatuba	-23.3449	-44.8478	0.46	1	71.9	150.27	490
MAUBA12	lotic	Ubatuba	-23.3487	-44.8527	0.15	1	80	10	100
MAUBA14	lotic	Ubatuba	-23.3581	-44.8272	0.6	2	80	127.99	320
MAUBA15	lotic	Ubatuba	-23.3528	-44.8552	1.2	1	40	328.461	450

Table S2: Backward elimination of variables from the full models of Linear Mixed-Effect Model to investigate the relationship between shifts in functional traits and the environmental characteristics of aquatic habitats. The response variable was functional space position in relation the first PCA axis (FSP1). The variables in the full models were: canopy cover, log area, depth, amount of aquatic vegetation. Variables with p-values >0.05 were dropped from the model.

Response variable	Covariate	LRT for variable
FSP1	Depth	df=7; LRT = 0.001; p=0.96
	Amount of aquatic vegetation	df=5; LRT=1.429; p=0.49
	logAREA	df=4; LRT= 0.272; p=0.60

Figure and legends

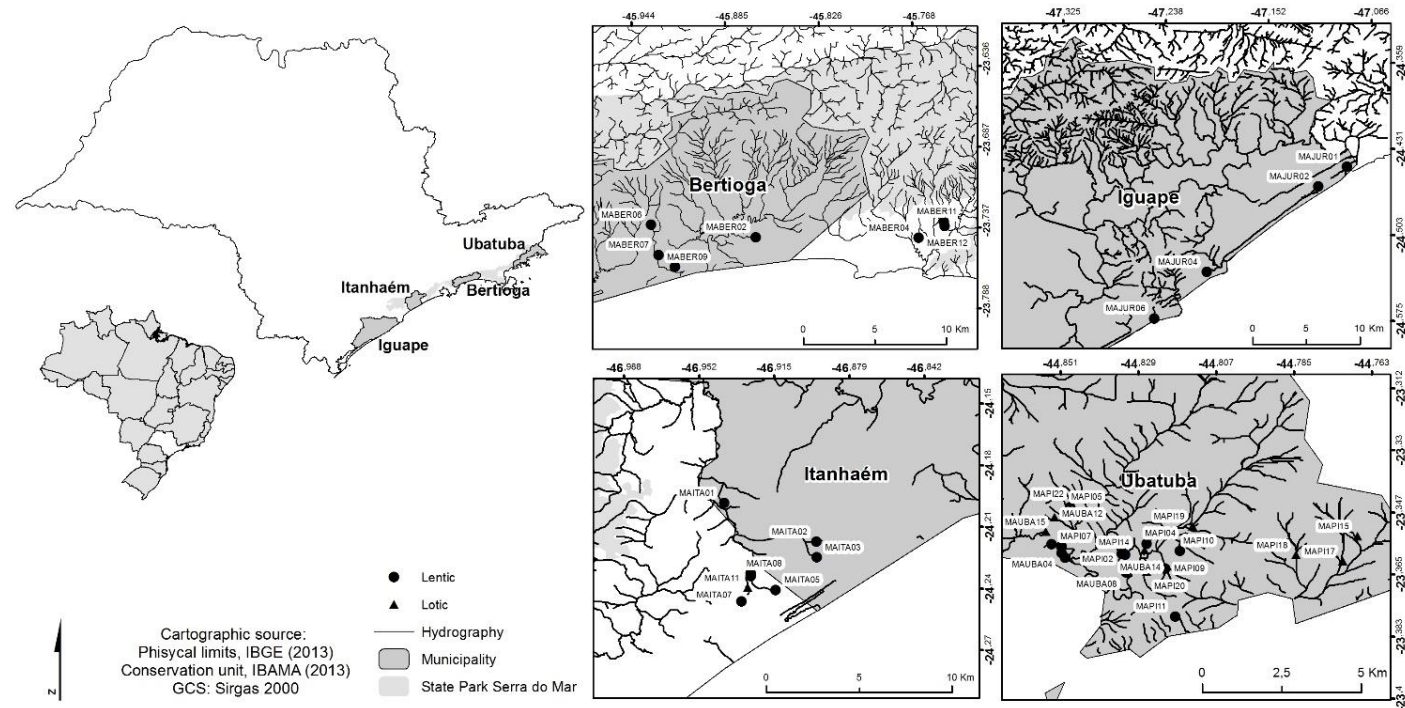


Figure 1: Geographical distribution of the 33 lentic and 10 lotic habitats in Atlantic Forest, sampled in four localities (Bertioga, Iguape, Itanhaém, and Ubatuba) in São Paulo state, Brazil. Circles and triangles represent, respectively, lentic and lotic habitats.

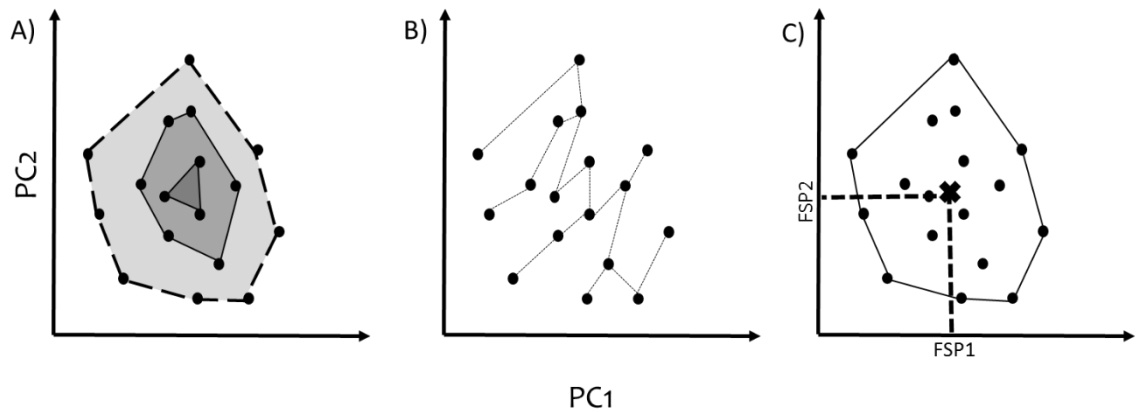


Figure 2: Functional metrics used to describe functional diversity in tadpole assemblages. The points that are plotted on the functional space formed by first and second principal components according to the trait values of each individuals of a community. **A)** The Functional Richness (FRic; Villéger *et al.*, 2008) is the total area of the polygon defined by the most extreme species drawn with dashed line. The Trait Onion Peeling (TOP; Fontana *et al.*, 2016) is the sum of all successive area of the polygon (in grayscales) touching all individuals within the functional space. **B)** The Functional Evenness (FEve; Villéger *et al.*, 2008) measures the regularity of the points beside of the minimum spanning tree (solid line). **C)** Functional Space Position (FSP) represents the center position of functional space for each community related to the first and second axes from PCA (FSP1 and FSP2, respectively).

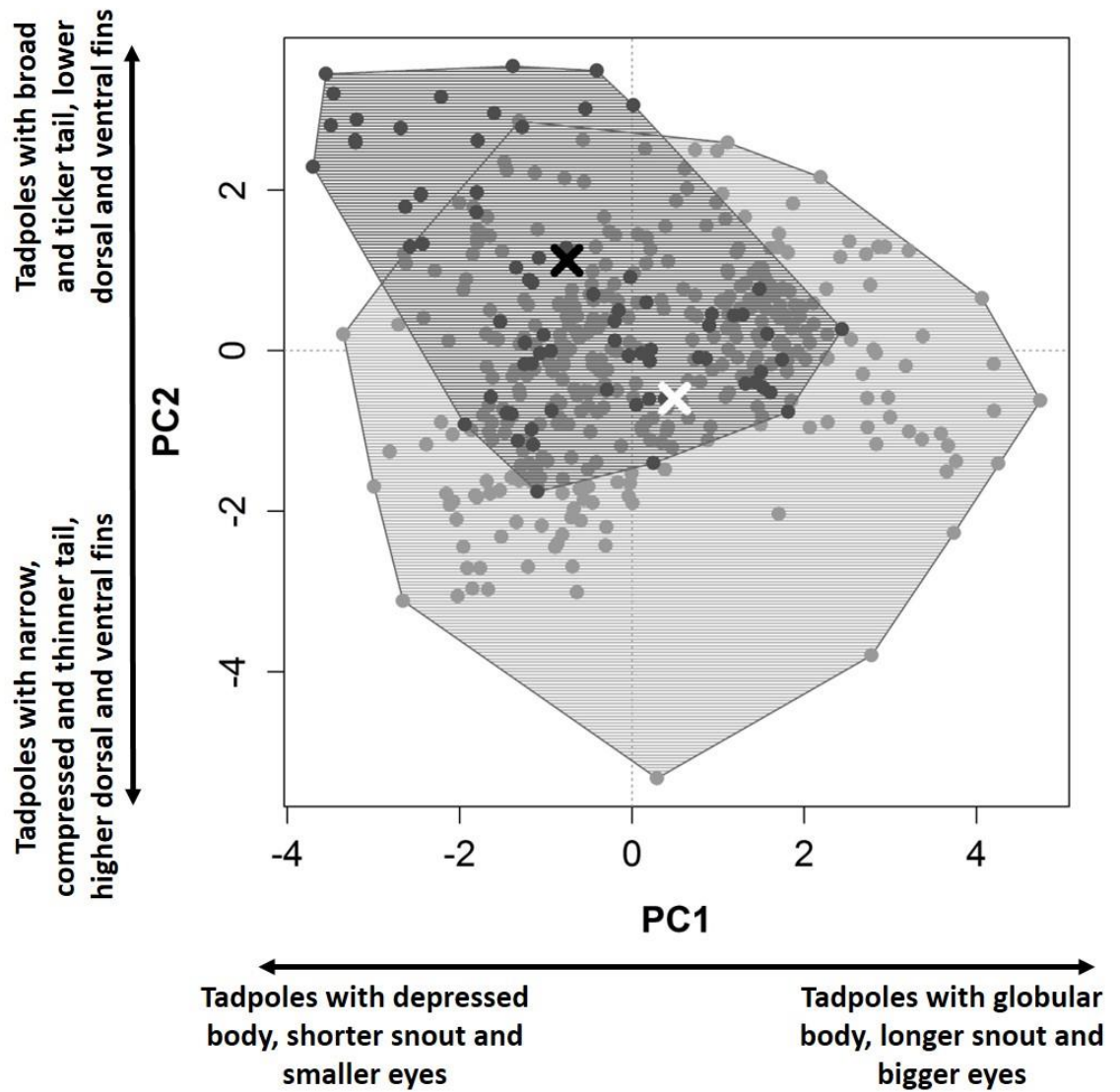


Figure 3: Biplot from Principal Component Analysis (PCA) to functional tadpoles traits. In light gray is represented the total functional space of lentic tadpoles, and in dark gray, the overall functional space of lotic tadpoles. The symbol 'X' is the centroid position of the total functional space for lentic tadpoles (in white) and lotic tadpoles (in black).

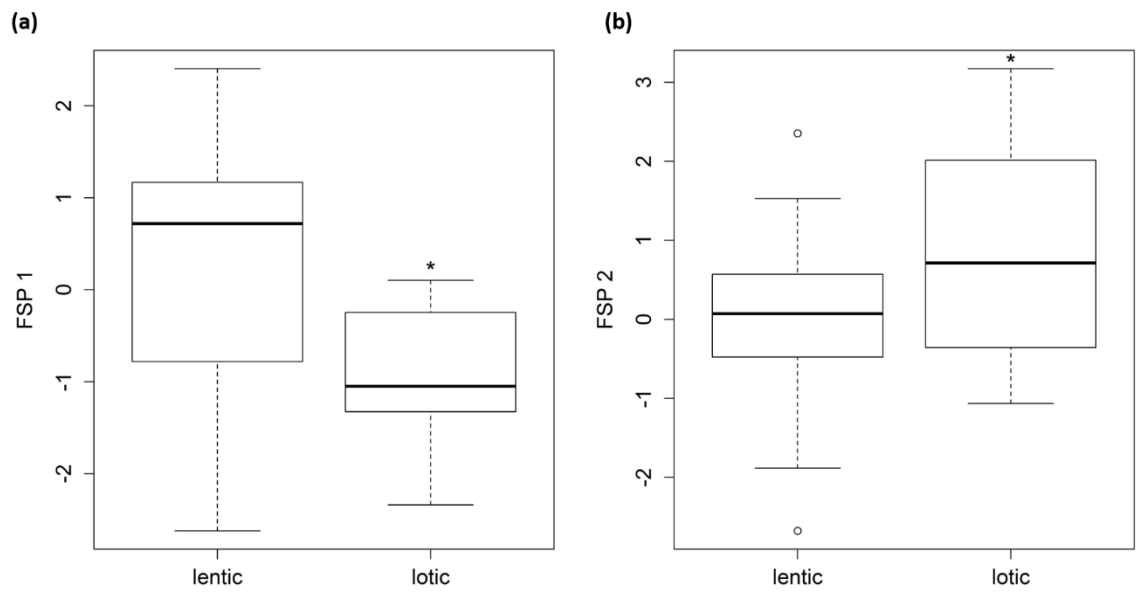


Figure 4: Difference in the functional space position (FSP) between lentic and lotic assemblages (a) in relation to the first, and (b) second axes obtained from Principal Component Analysis. * p-values < 0.05

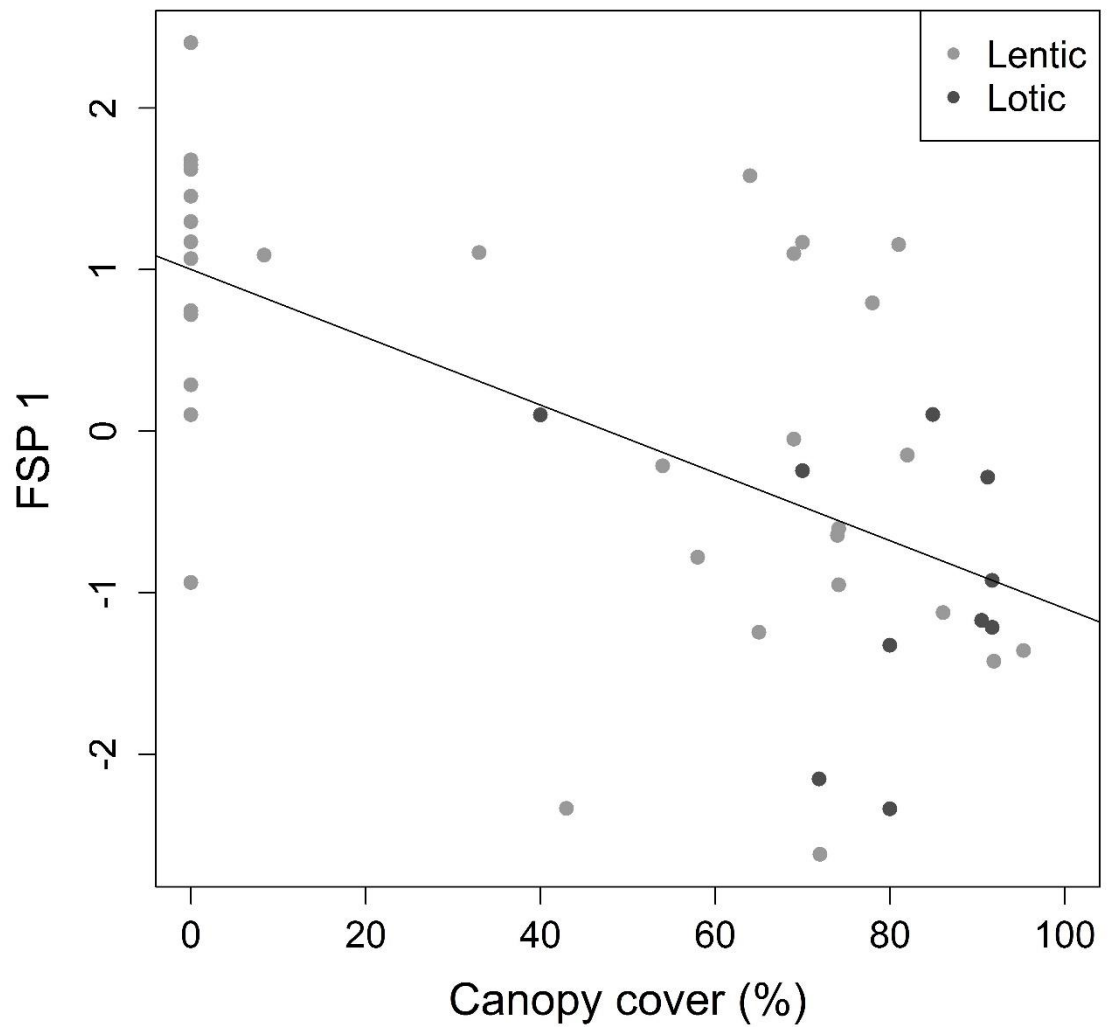


Figure 5: Relationship between canopy cover and Functional Space Position in relation of PC1 obtained from Principal Analysis Components (FSP1).

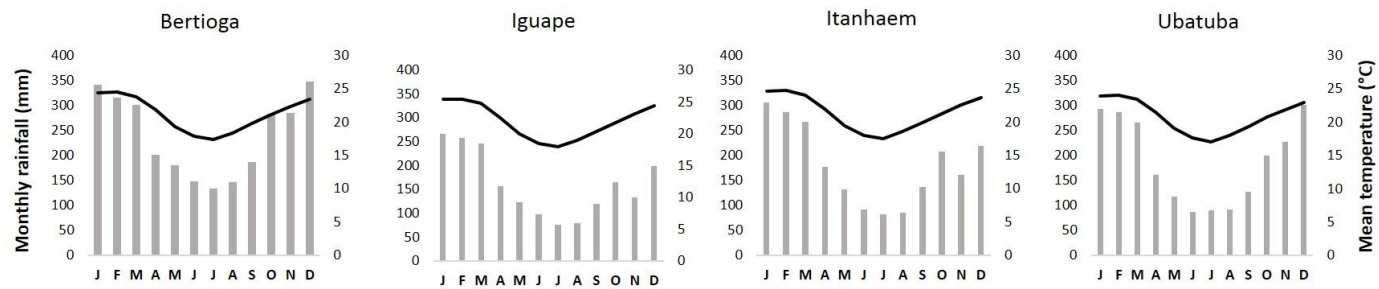


Figure S1: Monthly temperature and rainfall for the four localities: Bertioiga, Iguape, Itanhaém, Ubatuba, São Paulo state, Brazil. Data font: Alvares et al. 2013

CAPÍTULO 2

Intraspecific and interspecific trait variability in tadpoles
metacommunities from Tropical Rainforest**

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**Intraspecific and interspecific trait variability in tadpoles
metacommunities from Tropical Rainforest**

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Summary

1. A better understanding of the species coexistence and dynamics of communities may be benefited by adding information about the trait variability on individual and species levels.
2. Tadpoles assemblages offer an excellent system to understand the relative influence of intra- and interspecific variability in assembling communities, due to their ecosystem role, phenotypic plasticity, and the strong influence of environmental variables on their spatial distribution and performance.
3. Here we quantified the intra and inter-specific components of tadpoles traits variability and so, to investigate the role of both components of trait variation on the assembly of tadpoles' communities.
4. We selected eight functional traits related to microhabitat use, foraging strategies and swimming ability, measured at the individual level on 13 species of 31 ponds from Amazon and 22 species of 36 ponds from Atlantic Forest. We used single and multi-traits analyses to decompose the trait variability. To explore the action of external and internal filtering on assembly community we compared six components of phenotypic variability to null models.
5. On average, we detected 26% of intraspecific and 74% of interspecific phenotypic variability on tadpoles from Amazon and Atlantic Forests. The eight tadpoles traits differed in their amount of intra- and inter-specific variability, which are related to species niche difference (body shape, eyes size, and width of tail) and differences fitness (tail compression and height of dorsal fin). External filter influenced tadpoles assembly communities. The community variance in width of tail tadpoles is low in comparison to the total variance found in the region, evidencing that the individuals coexisting within

communities had been strongly filtered by abiotic conditions, regardless of species identity.

6. Our study emphasizes the importance to incorporate the functional intra- and interspecific trait variability to detection of the influence of intraspecific variability on assembly community and species coexistence.

Key-words: community assembly, ecological niche, fitness differences, phenotypic variability, stabilizing niche differences

Introduction

For decades, ecologists have been interested in understanding how species trait differences drive the assembly of communities. Though intraspecific trait variation - which combines genetic diversity and phenotypic plasticity - be at the origin of the theory of evolution, it has for a while been overlooked in trait-based ecology, that was searching for big patterns among species (Layman et al. 2015; Hart et al. 2016). Recent findings have re-emphasized the importance of intraspecific trait variation, as it can have tremendous effects on community structure and ecosystem functioning. For instance, intraspecific trait variation is expected to play a major role in community assembly processes (Violle et al. 2012), mediating species coexistence (Turcotte & Levine 2016) or determining the ability of natural systems to cope with environmental changes (Laurila et al. 2002; González-Suarez & Revilla 2013). The predictions from many general theories in ecology have been revisited in the light of intraspecific trait variation (e.g. Hart et al. 2016; Turcotte & Levine 2016) and tools have been developed to better encompass this supplementary level of information (e.g. Leps et al. 2011;

Carmona et al. 2012; Violle et al. 2012; Taudière et al. 2016). Although much of this research has focused on plants, there is also an increasing number of studies looking theoretically and empirically at the importance of intraspecific trait variation for competitive or trophic interactions in all types of organisms (Bolnick et al. 2011; Hughes et al. 2015; Zhao et al. 2014; Griffith et al. 2016).

The species coexistence is given by the balance between two major mechanisms: species fitness differences and stabilizing niche differences (Chesson 2000). While strong differences in traits related to fitness differences are predicted to determine the outcome of competitive exclusion, strong differences in traits related to stabilizing niche differences are expected to promote species coexistence. (Chesson 2000; Turcotte & Levine 2016). From a theoretical perspective, intraspecific phenotypic trait variability could enhance or impede species coexistence according to the magnitude of trait differences (Chesson 2000; Hart et al. 2016; Turcotte & Levine 2016). The trait variability promotes differences in the competitive ability between individuals which should decrease the intensity of competition between species and promote the coexistence (Hart et al. 2016; Turcotte & Levine 2016). In the other side, the high intraspecific variability can increase the niche overlap on species and then decrease the likelihood of coexistence in the absence of evolutionary changes (Hart et al. 2016; Turcotte & Levine 2016). From a methodological perspective, new frameworks such as the T-statistics variance ratios (Violle et al. 2012) has been applied to detect the markers of assembly processes and species coexistence while accounting for intraspecific trait variability (e.g. Bagousse-Pinguet et al. 2014; Neyret et al. 2016). Comparing the variance of trait value distributions at different scales (population, community, regional pool), this

framework allows detecting the effects of internal (microenvironmental heterogeneity and biotic interactions) and external (sorting of species from a regional pool due to large scale gradients) filters accounting the species mean or individuals difference (Violle et al. 2012).

These recent developments have not yet been applied to animal communities. Tadpoles meta-communities offer an excellent system to explore the role of intraspecific trait variation in trait-based community assembly processes. First, tadpoles have been found to exhibit extensive trait phenotypic plasticity, e.g. in timing and size at metamorphosis, morphology, physiology and behavior, in response to both physical environment (Eterovick & Barata 2006; Eterovick et al. 2010), and density of predators and competitors (Releya 2005; Michel 2012). Second, tadpoles represent the major part of biomass in freshwater habitats (Altig et al. 2007), they are important primary and secondary consumers, and as such are known to play a major role on ecosystem functioning (Strauß et al. 2010). In particular, by filter-feeding and grazing, they regulate the abundance and composition of algae communities and thus impact water quality and the primary productivity of the wetlands they inhabit (Whiles et al. 2006; Hocking & Babbitt 2014; Zongo & Boussim 2015). Third, though a good knowledge of tadpoles plasticity and response to environmental drivers under controlled conditions, there is still a backlog in our knowledge of the assembly of natural communities of amphibians at larval stage (Strauß et al. 2010; Grözinger et al. 2014).

Previous studies allow to identify four major environmental drivers to the spatial and temporal distribution of composition and diversity of larval anurans communities: 1) the water regime is crucial and temporary ponds and smaller

streams have been shown to host richer tadpoles communities (Skelly 1997; Eterovick 2003; Afonso & Eterovick 2007; Both et al. 2009); 2) species richness and composition are highly influenced by pond depth (Both et al. 2009) and ponds with intermediate water depth seem to host functionally more diverse communities (Queiroz et al. 2015); 3) the pond canopy cover strongly influence the distribution and performance of tadpoles (Skelly et al. 1999; Werner et al. 2007; Van Buskirk 2011; Provete et al. 2014); 4) predation pressure has been shown to alter the composition of tadpoles communities (Skelly 1997). Contrary to local environmental factors and stochasticity, it seems that biotic interactions play a minor role in shaping tadpoles communities (Kopp & Eterovick 2006; Strauß et al. 2010). In addition, previous studies have shown that tadpoles communities may encompass a low functional diversity and high levels of functional redundancy (large overlap in functional trait values) both among (Strauß et al. 2010) and within species (Eterovick 2003; Richter-Boix et al. 2007; Grözingen et al. 2014), mainly related to the ability to use a great diversity of microhabitats.

Here we propose for the first time to use a trait-based approach on tadpoles' communities to quantify the intra and inter-specific components of traits variation, investigating the role of intraspecific trait variation on the assembly of these communities. By analyzing a set of eight traits related to major components of stabilizing niche and fitness differences in tadpoles (microhabitat use, foraging strategies and swimming capacity) measured at the individual level on 13 species of 31 ponds from central Amazon, and 22 species of 36 ponds from Atlantic Rain Forest lowlands, we address two main questions:

• How is trait variation structured within and among species in tadpoles' communities for different major traits related to stabilizing niche and fitness differences in tadpoles? We predict that the eight traits will differ in their amount of intra- and inter-specific variations. We expect that the variation in traits related to stabilizing niche differences occur mainly in traits related to tadpoles water column position and the variation in traits related to average fitness differences occur mainly in traits representing swimming ability and chemical perception, thus sustaining communities with a high number of co-existing species (Turcotte & Levine 2016).

• What is the importance of external and internal filters in shaping the assembly of tadpoles' communities and which is the contribution of intra and interspecific trait variation involved in these processes? We expect external filters to play a major role on the communities' structure and internal filters to be less strong with high trait overlap among populations within a community (Eterovick 2003; Kopp & Eterovick 2006; Richter-Boix et al. 2007; Strauß et al. 2010; Grözinger et al. 2014).

Materials and methods

Study area

Tropical rainforests, found on different continents, are characterized by abundant rainfall, hot weather, and high species diversity. In South America, Amazon and Atlantic Forests are two of the top biodiversity hotspots (Myers et al. 2000; Jenkins et al. 2013) and are both under serious threat due to quick rates of

extensive deforestation. We sampled tadpole communities in both of these forests (Fig. 1).

The Amazon Forest, the largest tropical rainforest in the world, occupies half of the Brazilian territory, specifically in the North and part of the Center West region. The vegetation is characterized by Dense Ombrophilous Forest (IBGE 2012). We sampled communities in three different localities (Iranduba, Manaus, and Presidente Figueredo cities) in Amazonas state, Northern Brazil (Fig. 1). All localities have tropical climate, with no dry season (*Af* in Köppen Geiser classification, Alvares et al. 2013). The mean annual temperature is greater than 26°C. The annual rainfall is 2420 mm and the rainfall in the driest month is about 80 mm (Alvares et al. 2013).

Atlantic Rain Forest lowlands are distributed from 5 to 50 meters above sea level, between 16° to 24° latitude South (IBGE 2012), along Brazil coastal plains. The vegetation is characterized by macro- and meso-phanerophytes, lianas and epiphytes (IBGE 2012). We sampled communities in four different localities (Ubatuba, Bertioga, Itanhaém, and Iguape municipalities) in São Paulo state, Southeastern Brazil (Fig. 1). Bertioga, Iguape and Itanhaém have tropical climate, with no dry season (*Af* in Köppen Geiser classification, Alvares et al., 2013). The climate in Ubatuba is humid subtropical, with influence of the oceanic climate, with hot summers and no dry season (*Cfa* in Köppen Geiser classification, Alvares et al. 2013). Both climates are characterized by high temperatures (mean annual temperature: *Af* = 21.5 °C; *Cfa* = 20.8; Alvares et al. 2013) and high rainfall well distributed throughout the year (cumulative annual rainfall: *Af* = 2309 mm; *Cfa* = 2243 mm; Alvares et al. 2013).

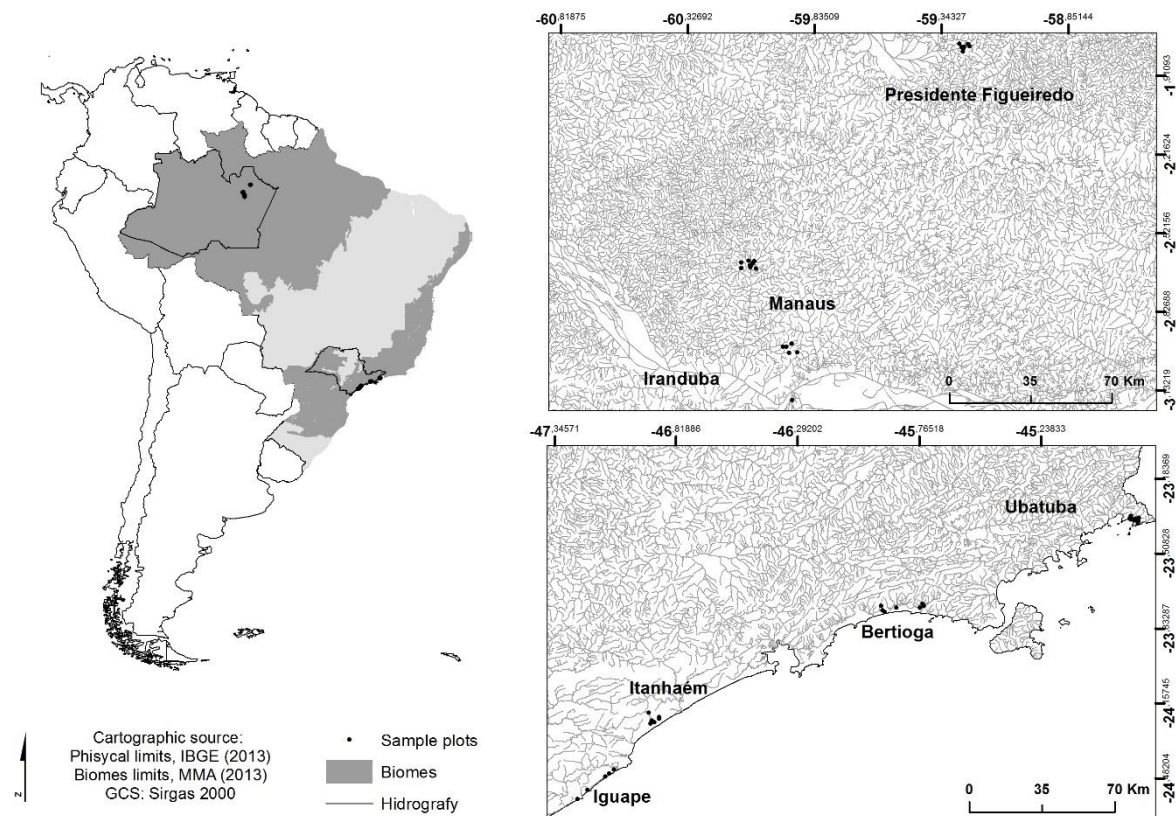


Figure 1: Geographical distribution of the 31 ponds in Amazon Forest, sampled in three localities (Iranduba, Manaus, and São Sebastião do Uatumã), in Amazonas state, and 36 ponds in Atlantic Forest, sampled in four localities (Bertioga, Iguape, Itanhaém, and Ubatuba), in São Paulo state, Brazil.

Database description

We used a subset of the database obtained by the Project “Tadpoles from Atlantic Forest, Amazon, Pantanal, Cerrado, and transition zones: morphological description, spatial distribution and diversity patterns” (SISBIOTA, grants CNPq 563075/2010-4 and FAPESP 2010/52321-7, 2011-2013). A standardized protocol was used to sample tadpole communities and characterize the 1,127 aquatic habitats in the different localities of this project. Tadpoles were sampled using a hand dip-net (32 cm diameter) with a 3 mm² mesh. Dip-net surveys were made throughout the total area of aquatic habitats to ensure a good representation of all the micro-habitats (Rossa-Feres & Jim 1996; Skelly & Richardson 2010).

Here we use a subset of 67 ponds from both Amazon and Atlantic Forests to address our questions. The ponds sampled in these two biomes represent the great variety of environmental conditions in the studies areas, presenting contrasting size, water depths, hydroperiod, amount of aquatic vegetation, substrate types on the bottom, and percentage of canopy cover (Table S1). All tadpoles collected during the SISBIOTA project were conserved in alcohol 70% and formaldehyde 15% solution (1:1) and deposited in scientific collections. Tadpoles from the Amazon Forest were deposited in “Paulo Bührnheim” collection from the Universidade Federal do Amazonas (UFAM), Manaus, Amazonas, Brazil, and tadpoles from the Atlantic Forest were deposited in DZSJRP Amphibia - Tadpoles collection of the Department of Zoology and Botany from the Universidade Estadual Paulista (UNESP), São José do Rio Preto, São Paulo, Brazil.

From these collections, we randomly selected and measured, depending on the availability, from one to 10 individuals in the developmental stages 33-37 (Gosner 1960), for each species occurring in each pond. Since tadpole abundance can reflect the aggregative behavior of tadpoles and large number of conspecific individuals can be found in a single pond (Hoff et al. 1999), we have established a maximum number of 10 individuals to minimize possible bias of measuring many siblings. Also, in order to minimize purely ontogenetic trait variability, we chose individuals from the developmental stages from 33 to 37 only (Gosner 1960), when changes in body parts of the tadpoles are isometric (Gosner 1960).

For the Amazon Forest, we measured traits of 60 tadpoles from 13 species (Table S2), found in 31 ponds. For the Atlantic Forest, we measured traits on 382

tadpoles from 22 anurans species (Table S3), registered in 36 ponds. These datasets were used to investigate the structuration of trait variation within and among species (question 1). To investigate the importance of external and internal filters in the assembly of tadpole communities we included only the tadpole communities with more than one species and more than one individual per species, which are the minimal requirements to calculate the T-statistics. Thus, to this analysis we reduced the Atlantic Forest dataset to a subset of 75 tadpoles from 8 species registered in 5 ponds. Alternatively, we also tested this hypothesis using data from 21 tadpoles communities with more than one species, regardless of the number of tadpoles per species.

Functional traits

Eight functional traits were obtained from the 10 morphological features we measured on each tadpole (Table 1). These traits are known to be related to essential elements of the ecology of tadpoles, namely resource use, as position in the water column (Altig & Johnston 1989; Alford 1999; Hoff et al. 1999; Van Buskirk 2009), body hydrodynamics, swimming ability (Altig & McDiarmid 1999), feeding behavior (Altig & Johnston 1989; Harris 1999), and chemical perception (Altig & McDiarmid 1999). All morphological features were measured in millimeters under a stereoscopic microscope with ocular micrometer (Leica MZ75).

259 **Table 1:** Functional traits measured on individual tadpoles from Amazon and Atlantic Forests.

Abbreviations	Trait index description	Biological interpretation	Ecological function
BCI	Body compression index = body height / body width	Higher values indicate globular body, and lower values, depressed body	Nektonic tadpoles have globular body. Benthic and nektonic tadpoles from family Microhylidae have depressed body (Altig & Johnston 1989; Altig & McDiarmid 1999; Van Buskirk 2009)
RDE	Relative diameter of the eyes = eye diameter / body length	Higher values indicate bigger eyes, and lower, smaller eyes	Nektonic tadpoles have larger eyes than benthic tadpoles (Altig & Johnston 1989; Altig & McDiarmid 1999)
HDF	Relative height of the dorsal fin = maximum dorsal fin height / body height	Higher values indicate higher fin, and lower values lower fin	Nektonic tadpoles have high dorsal fins which keep them in equilibrium and facilitates their displacement in the water column. Benthic tadpoles have low dorsal fins (Hoff & Wassersug 2000; Altig & Johnston 1989; Altig & McDiarmid 1999)
HVF	Relative height of the ventral fin = maximum ventral fin height / body height	Higher values indicate higher fin, and lower values lower fin	Nektonic tadpoles have higher ventral fins than benthic tadpoles, which keep them in equilibrium and facilitates their displacement in the water column (Altig & Johnston 1989; Altig & McDiarmid 1999)
RWT	Relative width of the tail = tail muscle width / body width	Higher values indicate broad tail muscle, and lower values, narrow tail muscle	Nektonic tadpoles have narrow tail muscle. Benthic tadpoles have broad tail muscle, facilitating they escape from active predators and their displacement on the bottom (Altig & McDiarmid 1999; Van Buskirk & Relyea 1998; Van Buskirk 2009)

261 **Table 1:** Continuation. Functional traits measured on individual tadpoles from Amazon and Atlantic Forests.

Abbreviations	Trait index description	Biological interpretation	Ecological function
TCI	Tail compression index = tail muscle height / tail muscle width	Higher values indicate compressed and thinner tail, and lower values, thicker tail	Variations in muscle tail reflect different position in the water column, swimming mechanics and styles. Pond- dwelling tadpoles have thinner and more flexible tail (Altig & McDiarmid 1999)
DNS	Distance from nares to snout	Higher values indicate nares closer to eyes and lower values anterior to nares (closer to snout)	Position of nares is related to chemical perception. Anterior nares facilitate the search for food resources and detection of chemicals cues of predators (Altig & McDiarmid 1999)
RDN	Relative diameter of the nares = nares diameter / body length	Higher values indicate bigger nares, and lower, smaller nares	Variations in nares diameter is related to chemical perception of smells due to, in bigger nares, circulates larger volume of water (Altig & McDiarmid 1999)

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Data analysis

Decomposition of trait variation

In order to decompose the variation of traits within and among species, we used two complementary approaches following Albert et al. (2010): single-trait (linear mixed models) and multi-traits analyses (between principal component analyses). As different numbers of individuals and populations have been sampled for each species, we used a re-sampling procedure to balance the data sets (equal number of individuals) for both Amazon and Atlantic Forests data. Initially, we determined the smallest number of individuals measured within species ($n=3$ for both biomes). After, we subsampled the original dataset by drawing randomly 1000 balanced data subsets containing the smallest number of individuals per species (Albert et al. 2010). This subsampled data was used to perform the single and multi-trait analyses.

For the single-trait approach, we used linear mixed models with restricted maximum likelihood estimation (Albert et al. 2010; Messier et al. 2010; Auger & Shipley 2013). We constructed the models to test the intra and interspecific variability for each trait, including no fixed effect and species as a random effect (trait $\sim (1 \mid \text{species})$). The percentage of variability attributed to each level (intra and interspecific) was expressed as percentage of the total variance.

For the multi-trait approach, we used between- and within-groups principal components analyses to decompose the variance for the eight traits simultaneously (Albert et al. 2010). Between-species PCA uses the correlation matrix based on species means (weighted by their sample size) and finds linear combinations of variable maximizing the between-species variance instead of the overall variance (Dodélec & Chessel 1991). The inertia calculated in a between

PCA represents the part of the total variance due to the differences between species (Dodélec & Chessel 1991). A between PCA ($BPCA_{\text{between}}$ mean) results after a re-sampling procedure on the whole data set will show the relative importance of within- and between-species variances, while between PCAs on each species ($BPCA_{\text{within}}$) will give the decomposition between and within populations (Albert et al. 2010).

Importance of external and internal filters in shaping tadpole communities

In order to assess the importance of external and internal filtering in shaping tadpole communities and the importance of intraspecific trait variability in these processes, we calculated the recently proposed T-statistics framework (Violle et al. 2012). Six components of traits variance can be identified (from individual trait measurements): 1) variance of trait values among individuals within populations (σ_{IP}^2); 2) variance of trait values among individuals within communities (σ_{IC}^2); 3) variance of trait values among individuals within the regional pool (σ_{IR}^2); 4) variance of population mean trait values within communities (σ_{PC}^2); 5) variance of population mean trait values within the regional pool (σ_{PR}^2); and 6) variance of community mean trait values within the regional pool (σ_{CR}^2). T-statistics are ratios of these components that depict how some subsets of the trait variance are organized across spatial and biological levels. 1) $T_{IP,IC}$ is the observed ratio between variance of individuals' trait values in populations (σ_{IP}^2) and variance of individuals' trait values in communities (σ_{IC}^2). It quantifies how the distribution of individual trait values within populations overlap with the distribution of individual trait values within communities, i.e. niche

packing of species within communities, and reflects the strength of internal
 filtering affecting individuals. Values of $T_{IP,IC}$ close to 1 (respectively close to 0)
 indicate low (respectively high) levels of internal filtering (Violle et al. 2012). 2)
 $T_{IC,IR}$ is the observed ratio between variance of individuals' trait values in
 communities (σ_{IC}^2) and variance of individuals' trait values in the regional pool
 (σ_{IR}^2). It quantifies how the distribution of individual trait values within
 communities overlap with the regional distribution of individual trait values, and
 thus reflects the strength of external filtering at the individual level. 3) $T_{PC,PR}$ is the
 observed ratio between variance of population trait values in communities (σ_{PC}^2)
 and population trait values in the region (σ_{PR}^2). It quantifies how the distribution
 of population mean trait values within communities overlap with the regional
 distribution of population mean trait values, and thus reflects the strength of
 external filtering at the population levels. For both, $T_{IC,IR}$ and $T_{PC,PR}$, values close
 to 1 (respectively 0) indicate little (respectively strong) external filtering (Violle et
 al. 2012). To determine the significance of the T-statistics we compared the
 observed values with null models using standardized effect sizes with 9
 replications (SESS) (Taudière & Violle 2016). To test the potential effects of
 species richness on the observed niche packing, we explored the correlations
 between T-statistics and species richness (Fig. S1 and S2).

All statistics analysis we performed in R 3.3.1 (R Core Team 2016) using
 different packages: lme4 (Bates et al. 2015) for mixed models, ade4 (Dray &
 Dufour 2007) for multivariate analyses, and cati for the T-statistics (Taudière &
 Violle 2016).

Results

How is trait variation structured within and among species?

Single- and multi-trait analyses led to similar average results regarding the relative contributions of intra- (~25%) and inter-specific (~75%) trait variability to the total trait variability in tadpoles from Amazon and Atlantic Forests (Table 2). However, the decomposition strongly differed among traits and among regions. For Amazon Forest, the tail compression index (TCI) showed a high contribution of intraspecific variability (>85%) while for all remaining traits the contribution of intraspecific variability to total trait variation was low (<25%, Table 2). For Atlantic Forest, the height of dorsal fin (HDF) and tail compression index (TCI) showed equivalent contributions of intra- and interspecific variability (Table 2) while for all the others traits the contribution of intraspecific variability to total trait variation was low (<26%, Table 2).

From the within-species PCA the same traits explained most of intraspecific variation in tadpoles traits. For Amazon Forest the functional trait variability was structured by a first axis (56% of variation) mainly driven by tail compression index (TCI), and a second axis (13.8%) mainly driven by height of dorsal fin (HDF; Fig. 2). For Atlantic Forest, the tadpoles trait variability was structured by a first axis (34% of variation) mainly driven by height of dorsal fin (HDF), and a second axis (22.6% of variation) mainly driven by tail compression index (TCI; Fig. 2).

From the between-species PCA for Amazon Forest, tadpoles functional trait variability was structured by a first axis (62% of variance) mainly driven by relative width of the tail (RWT), distance from nares to snout (DNS), height of

ventral fin (HVF), relative diameter of the nares (RDN), and diameter of eyes (RDE), and a second axis (17% of variation) mainly driven by body compression index (BCI) and height of dorsal fin (HDF; Fig. 2). From the between-species PCA for the Atlantic Forest, tadpoles functional trait variability was structured by a first axis (35% of variation) mainly related to body compression index (BCI), diameter of eyes (RDE), and width of tail (RWT), and a second axis (24% of variation) related to distance from the nares to snout (DNS) and height of ventral fin (HVF; Fig. 2).

Table 2: Percentage of variance decomposition in intraspecific and interspecific contribution for each tadpoles from Amazon and Atlantic Forest trait and the total average for single and multi-trait analyses. Mean results after a re-sampling procedure. Square brackets represent the 95% confidence intervals. Bold values represent the greater intra or interspecific variability for each biome.

Functional traits	Amazon		Atlantic Forest	
	Intraspecific variability	Interspecific variability	Intraspecific variability	Interspecific variability
Body compression index	0.25 [0.25 - 0.25]	0.74 [0.74 - 0.75]	0.15 [0.14 - 0.15]	0.85 [0.85 - 0.85]
Relative diameter of the eyes	0.10 [0.09 - 0.11]	0.90 [0.89 - 0.90]	0.21 [0.20 - 0.21]	0.79 [0.78 - 0.79]
Relative height of the dorsal fin	0.16 [0.16 - 0.17]	0.83 [0.83 - 0.84]	0.47 [0.46 - 0.48]	0.53 [0.52 - 0.53]
Relative height of the ventral fin	0.23 [0.23 - 0.23]	0.76 [0.76 - 0.77]	0.26 [0.25 - 0.26]	0.74 [0.74 - 0.75]
Relative width of the tail	0.02 [0.02 - 0.02]	0.98 [0.98 - 0.98]	0.18 [0.18 - 0.18]	0.82 [0.81 - 0.82]
Tail compression index	0.86 [0.85 - 0.87]	0.14 [0.13 - 0.15]	0.51 [0.51 - 0.512]	0.49 [0.48 - 0.50]
Distance from nares to snout	0.03 [0.03 - 0.04]	0.96 [0.96 - 0.96]	0.11 [0.11 - 0.11]	0.89 [0.89 - 0.89]
Relative diameter of the nares	0.18 [0.18 - 0.19]	0.82 [0.81 - 0.82]	0.23 [0.23 - 0.24]	0.76 [0.76 - 0.77]
Average of single-trait analysis	0.25	0.82	0.26	0.62
Average of multi-trait analysis	0.20	0.80	0.30	0.69

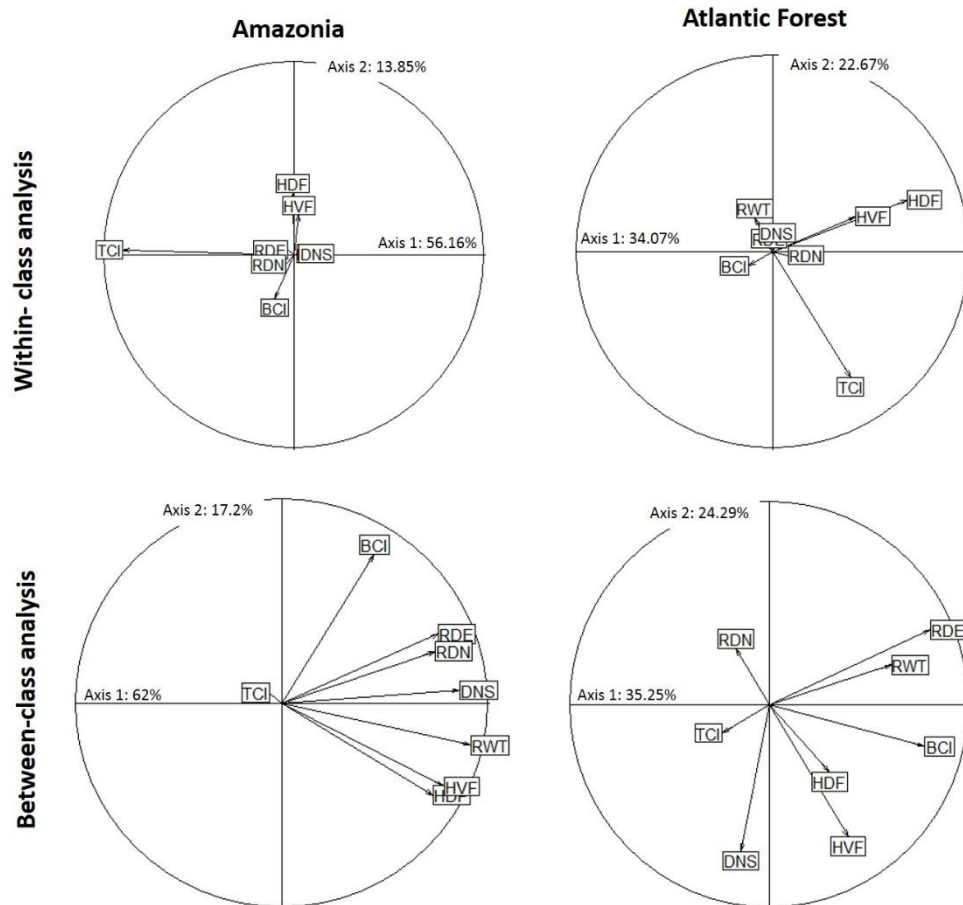


Figure 2: Correlation circles regarding the first two axes of within-species and between-species PCA on functional traits for tadpoles communities of Amazon and the Atlantic Forests

What is the importance of external and internal filters in shaping tadpole communities?

Regarding internal filtering, the mean SES for T-statistic $T_{IP.IC}$ was lower than expected by the null model for all the traits, except for height of the dorsal fin and tail compression index (Fig. 3). This is a sign of non-overlapping trait distributions among species within communities. The pattern of $T_{IP.IC}$ of most communities was similar to the mean SES, except for ponds BER2 and UPI5 for height of dorsal fin and nares size (Fig. 3).

Regarding external filtering at the individual level, the mean SES for T-statistics $T_{IC.IR}$ was lower than expected by the null model for the width muscle

tail (RWT). The individual trait variability in the communities was lower than the variability of all individuals in the region (Fig. 3). The pattern of $T_{IC,IR}$ of most communities was similar to the mean SES, excepted for BER11 and BER2 for size eyes, JUR01 for height of fins, and UPI12 for distance from nares to snout. This indicates that the individual trait variability in the communities was close to the variability of all individuals in the region.

Regarding external filtering at the species level, the mean SES for T-statistic $T_{PC,PR}$ was globally not different from the null model expectations for all the traits (Fig. 3). Only some communities slightly deviate from the null expectation: the pond UPI5 related to the body and tail compression and height of ventral fin; the pond UPI12 close to zero for tail compression and close to 1 for distance of nares (Fig.3). Considering the 21 tadpoles communities the results differed just related to the internal filtering. The mean SES for T-statistic $T_{IP,IC}$ was lower than expected by the null model for all the traits, except for relative diameter of nares (Fig. S3).

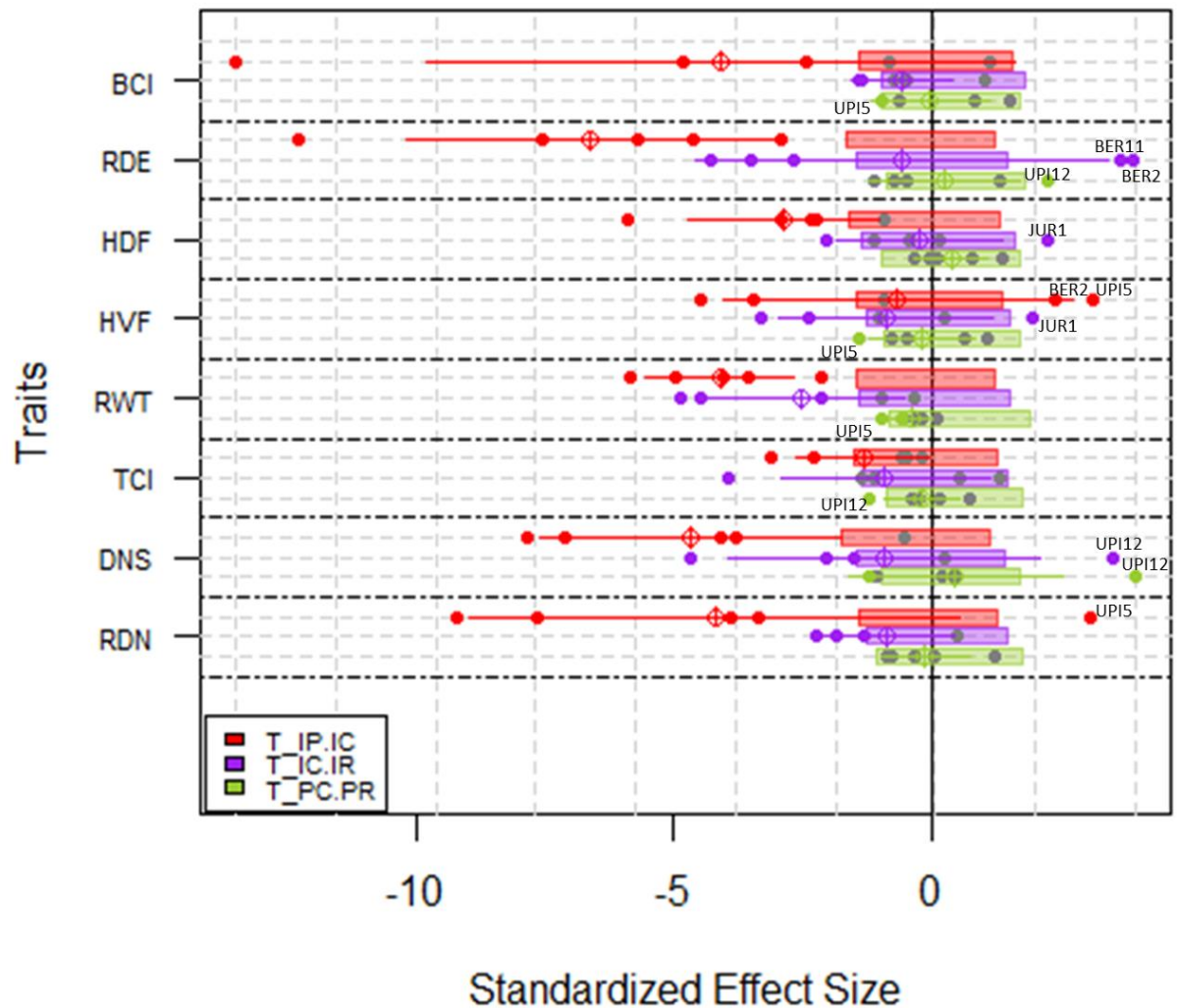


Figure 3: Standardize effect size (SES) of T-statistics for eight functional traits: BCI = Body compression index; RDE = Relative diameter of the eyes; HDF= Relative height of the dorsal fin; HVF = Relative height of the ventral fin; RWT = Relative width of the tail; TCI = Tail compression index; DNS = Distance from nares to snout; RDN = Relative diameter of the nares. The three ratios of variance are: i) $T_{IP.IC}$ – ratio of within population variance to total within community variance; ii) $T_{IC.IR}$ – community-wide variance relative to the total variance in the regional pool; iii) $T_{PC.PR}$ – inter-community variance relative to the total variance in the regional pool. Dot represents the SES values for each community. The crossed circles represent the mean SES values and the segments represent the standard deviation of the SES values. The mean of SES (crossed circles) is significantly different from the null distribution when it is not embedded within the box. The communities identified are different that found by the general patterns.

Discussion

Besides the interspecific variability, we found a not negligible intraspecific variability in tadpoles communities from Amazon and Atlantic Forests. Our study is one of the first to test empirically the quantity of inter- and intraspecific components in animals assemblages, finding a similar pattern of intraspecific variability in plants, with around 30% of mean intraspecific variation (Jung et al. 2010; Albert et al. 2010; Messier et al. 2010; de Bello et al. 2011). For instance, Siefert et al. (2015) have shown that around $\frac{1}{4}$ of trait variation in commonly used plant functional traits occur within species. Our results show a higher intraspecific variability than found in invertebrate's traits. Despite the fact that dung beetle to display greater interspecific than intraspecific variability (Griffiths et al. 2016), consider both components of trait variation can better predict the action of ecological filters in assembly community than represent the species by mean trait values (Albert et al. 2010).

According to our expectation, the eight tadpoles traits differed in their amount of intra- and inter-specific variability. Even used a multi-trait approach the results were congruent between biomes to each functional trait. In general, the intraspecific variability in tadpoles traits for Amazon and Atlantic Forests was mainly related to height of dorsal fin and tail compression. The interspecific variability was mainly related to all the others traits, such as body shape, nares position and size, and relative width of tail, which had an important effect of internal filtering. Regarding the external filtering, our results show a strong effect of external filtering in the width of tadpoles muscle tail.

Tadpoles tails traits, which presented greater intraspecific variability influence the individual swimming performance (Van Buskirk & McCollum 2000) which can be affect by morphological (body shape and configuration of tails and body) and physiological (muscular activities) changes in aquatic organisms (Wassersug & Hoff 1985; Doerthy et al. 1998; Hoff & Wassersug 2000). Many studies report that tail of tadpoles present high phenotypic plasticity (Relyea 2002; Miner et al. 2005) mainly due to the predation pressure (Smith & Van Buskirk 1995; Van Buskirk & Schmidt 2000, Van Buskirk & McCollum 2000). Tadpoles tend to develop large tails and smaller bodies when they are under predation pressure (Van Buskirk & McCollum 2000; Relyea 2002), increasing the individual performance by changes in swimming speed and acceleration allowing tadpoles to escape to predator attack (Van Buskirk & McCollum 2000). Therefore, our results might indicate that the greater intraspecific tail tadpoles traits variability can be related species fitness differences.

However, as theoretically predicted, only species fitness differences cannot promote coexistence. The differences in ecological niche should be greater than fitness differences (Chesson 2000; Turcotte & Levine 2016). In opposite to our expectation, we detected low trait overlap among populations within a community. We detected higher interspecific variability related to body shape, eyes, width tail, and nares sizes in tadpoles communities from Atlantic Forest. The variability within population was lower than among species in the community, indicating few intraspecific and high interspecific variability. The tadpoles body shape, eyes size, and width of tail reflect the ability to foraging in different position along the water column (Eterovick & Barros 2003; Kopp & Eterovick 2006). Whereas the size and location of nares reflect the ability

perception chemicals related to food acquisition and predator avoidance (Altig & Johnston 1989). Tadpoles with bigger nares and closer to snout can detect chemicals signals faster. These results reinforce that the differences between species are mainly linked to niche differences, suggesting the potential influence of niche packing process (Violle et al. 2012), in which coexisting species fill the available 'space' along important niche dimensions (Violle et al. 2012).

We detected evidences of external filter on the tadpoles assembly communities related to the width of tail. Our results show that the community variance in width of tail tadpoles is low in comparison to the total variance found in the region, evidencing that the individuals coexisting within communities had been strongly filtered by abiotic conditions, regardless of species identity. In the region is possible to find tadpoles with different tail width, but in each community, there is a filter selecting tadpoles with specific relative width of tail. The width of tail differs between tadpoles with broad and narrow tail. The influence of external filter in the width of tail muscle tail can be an evidence of segregation among species of different ecomorphological guilds. In the case, nektonic tadpoles, which exhibit narrow tail muscle, and benthic tadpoles which have broad tail muscle did not occur in the same pond. There are evidences that shallow ponds harbor only benthic tadpoles (Queiroz et al. 2015). However, this result should be interpreted with prudence due to the presence of many individuals and few species in the communities. Moreover, these results highlighted the importance of ecological studies to test the effect of environmental conditions in the components of traits variance.

Due to the protocol used we did a partial sampling of intraspecific variation, selecting tadpoles in the development stage from 33 to 37 to control the

ontogenetic variability, we may have underestimated the degree of overlap between species (Violle et al. 2012). Nevertheless, our study emphasizes the importance to incorporate the functional intra- and interspecific trait variability to detection of the influence of intraspecific variability on assembly community and species coexistence, not only for studies with plants, but also with animals communities. In this study, we did not detect any effect of ecological filters considering the species variability (average differences between species). These results show that external filtering detected at the individual level is not detectable at the population level.

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Supporting Information

Table S1: Environmental variables for the 67 ponds studied in Amazon and Atlantic Forests. Highlighted the communities selected to T-statistic procedure with (♦) five and (‡) 21 communities.

Site	Biome	Localities	Latitude	Longitude	Depth (cm)	Amount of aquatic vegetation	Canopy cover (%)
FE1	Amazon	Manaus	-2.63581	-60.121	0.09	3	8
FE2	Amazon	Manaus	-2.64836	-60.0873	0.08	3	3
FE3	Amazon	Manaus	-2.64836	-60.0873	0.05	3	15
FE4	Amazon	Manaus	-2.64836	-60.0873	0.08	3	17
FE5	Amazon	Manaus	-2.64836	-60.0873	0.05	3	15
FE6	Amazon	Manaus	-2.64783	-60.0826	0.1	3	13
FE7	Amazon	Manaus	-2.63977	-60.0768	0.03	3	4
FE8	Amazon	Manaus	-2.62989	-60.0925	0.08	3	31
FE9	Amazon	Manaus	-2.62989	-60.0925	0.07	3	36
FE10	Amazon	Manaus	-2.66022	-60.0626	0.1	3	9
FE11	Amazon	Manaus	-2.65799	-60.121	0.05	3	21
FE12	Amazon	Manaus	-2.65563	-60.0845	0.09	3	38
FE13	Amazon	Manaus	-2.63075	-60.0693	0.09	3	23
FE14	Amazon	Manaus	-2.63075	-60.0693	0.08	3	19
LC1	Amazon	Iranduba	-3.16983	-59.9232	6.32	3	0
RB1	Amazon	Presidente Figueiredo	-1.79861	-59.2569	0.2	3	15
RB2	Amazon	Presidente Figueiredo	-1.78958	-59.2405	0.03	3	17
RB3	Amazon	Presidente Figueiredo	-1.80028	-59.2657	0.2	3	20
RB4	Amazon	Presidente Figueiredo	-1.80028	-59.2657	0.05	3	16
RB5	Amazon	Presidente Figueiredo	-1.80714	-59.2599	0.06	3	18
RB6	Amazon	Presidente Figueiredo	-1.79736	-59.234194	0.22	3	13

Table S1: Continuation. Environmental variables for the 67 ponds studied in Amazon and Atlantic Forests. Highlighted the communities selected to T-statistic procedure with (♦) five and (‡) 21 communities.

Site	Biome	Localities	Latitude	Longitude	Depth (cm)	Amount of aquatic vegetation	Canopy cover (%)
RB7	Amazon	Presidente Figueiredo	-1.81714	-59.2605	0.11	3	15
RB8	Amazon	Presidente Figueiredo	-1.81714	-59.2605	0.15	3	16
RB9	Amazon	Presidente Figueiredo	-1.78784	-59.2749	0.09	3	17
RB10	Amazon	Presidente Figueiredo	-1.789	-59.2408	0.59	3	17
RF1	Amazon	Manaus	-2.96322	-59.9584	0.1	3	38
RF2	Amazon	Manaus	-2.95101	-59.9246	0.17	3	16
RF3	Amazon	Manaus	-2.95101	-59.9246	0.05	3	24
RF4	Amazon	Manaus	-2.96397	-59.9453	0.07	3	18
RF5	Amazon	Manaus	-2.98525	-59.9037	0.15	3	4
RF6	Amazon	Manaus	-2.98632	-59.9359	0.12	3	98
BER2♦‡	Atlantic Forest	Bertioga	-23.7433	-45.8655	1.5	3	0
BER4	Atlantic Forest	Bertioga	-23.7438	-45.7634	1.1	3	54
BER6‡	Atlantic Forest	Bertioga	-23.7355	-45.9312	1.2	3	69
BER7	Atlantic Forest	Bertioga	-23.7544	-45.9265	1.1	3	64
BER9‡	Atlantic Forest	Bertioga	-23.762	-45.9163	1.6	3	33
BER10‡	Atlantic Forest	Bertioga	-23.7265	-45.7528	0.4	3	0
BER11♦‡	Atlantic Forest	Bertioga	-23.7336	-45.7476	1.1	3	78
BER12‡	Atlantic Forest	Bertioga	-23.7362	-45.7471	0.6	3	0
ITA1‡	Atlantic Forest	Itanhaem	-24.1986	-46.9394	0.27	3	0
ITA2	Atlantic Forest	Itanhaem	-24.2173	-46.8946	0.4	3	0
ITA3	Atlantic Forest	Itanhaem	-24.2249	-46.8944	1.5	3	0
ITA4‡	Atlantic Forest	Itanhaem	-24.2341	-46.9264	0.45	3	81
ITA5	Atlantic Forest	Itanhaem	-24.2407	-46.9144	0.25	3	0
ITA7	Atlantic Forest	Itanhaem	-24.2463	-46.931	2	3	0
ITA8	Atlantic Forest	Itanhaem	-24.2326	-46.9265	1.6	3	70
JUR1♦‡	Atlantic Forest	Iguape	-24.4444	-47.0903	1	3	65
JUR2‡	Atlantic Forest	Iguape	-24.4621	-47.1104	0.8	3	74
JUR3	Atlantic Forest	Iguape	-24.4747	-47.1266	4	3	0
JUR4‡	Atlantic Forest	Iguape	-24.5338	-47.2039	0.95	3	0

Table S1: Continuation.

Site	Biome	Localities	Latitude	Longitude	Depth (cm)	Amount of aquatic vegetation	Canopy cover (%)
JUR6	Atlantic Forest	Iguape	-24.5728	-47.2478	0.65	3	43
UPI1‡	Atlantic Forest	Ubatuba	-23.3701	-44.817	0.29	1	78.4
UPI2‡	Atlantic Forest	Ubatuba	-23.3591	-44.8336	0.46	2	8.4
UPI3‡	Atlantic Forest	Ubatuba	-23.3556	-44.8158	0.18	1	0
UPI4‡	Atlantic Forest	Ubatuba	-23.3459	-44.8483	0.3	1	74.15
UPI5♦‡	Atlantic Forest	Ubatuba	-23.3571	-44.8508	0.3	1	74.15
UPI7	Atlantic Forest	Ubatuba	-23.3633	-44.8214	0.56	2	95.3
UPI8‡	Atlantic Forest	Ubatuba	-23.3583	-44.8172	0.14	2	86.1
UPI9	Atlantic Forest	Ubatuba	-23.3769	-44.8185	0.86	1	91.9
UPI10	Atlantic Forest	Ubatuba	-23.3538	-44.8149	0.75	1	96.1
UPI11‡	Atlantic Forest	Ubatuba	-23.3588	-44.8335	0.4	2	0
UPI12♦‡	Atlantic Forest	Ubatuba	-23.3602	-44.8498	1.3	3	58
UPI13	Atlantic Forest	Ubatuba	-23.3589	-44.8507	0.6	3	69
UPI14	Atlantic Forest	Ubatuba	-23.3593	-44.8327	0.1	3	0
UPI15	Atlantic Forest	Ubatuba	-23.3563	-44.8266	0.6	3	72
UPI16‡	Atlantic Forest	Ubatuba	-23.3644	-44.8324	0.5	3	0
UPI17‡	Atlantic Forest	Ubatuba	-23.3564	-44.8536	0.25	3	82

Table S2: Larval anuran species found in 31 ponds in Central Amazon (Amazonas state, Brazil). Total abundance of individuals collected for the project SISBIOTA (all stages of development). Number of individuals measured from the stages 33-37.

Family	Species	Total abundance	Number of individuals measured
Aromobatidae	<i>Allobates femoralis</i>	1	0
	<i>Allobates sumtuosus</i>	533	30
Bufonidae	<i>Amazophrynella manaos</i>	11	3
	<i>Rhinella proboscidea</i>	22	1
Dendrobatidae	<i>Ameerega hahneli</i>	2	0
	<i>Dendropsophus brevifrons</i>	4	2
	<i>Dendropsophus nanus</i>	27	9
Hylidae	<i>Hypsiboas cinerascens</i>	1	1
	<i>Hypsiboas fasciatus</i>	37	4
	<i>Hypsiboas raniceps</i>	3	1
	<i>Osteocephalus taurinus</i>	7	2
	<i>Phyllomedusa bicolor</i>	26	1
	<i>Sphaenorhynchus carneus</i>	1	1
Leptodactylidae	<i>Leptodactylus rhodomystax</i>	24	3
Microhylidae	<i>Chiasmocleis hudsoni</i>	2	2

Table S3: Larval anuran species found in 36 ponds in the Atlantic Rain Forest lowlands (São Paulo state, Brazil). Total abundance of individuals collected for the project SISBIOTA (all stages of development). Number of individuals measured from the stages 33-37.

Family	Species	Total abundance	Number of individuals measured
Bufonidae	<i>Rhynella ornata</i>	3039	24
	<i>Aplastodiscus eugenioi</i>	43	19
	<i>Dendropsophus berthalutzae</i>	33	7
	<i>Dendropsophus elegans</i>	230	12
	<i>Dendropsophus gisleris</i>	1	0
	<i>Dendropsophus microps</i>	18	4
	<i>Dendropsophus minutus</i>	165	9
	<i>Dendropsophus werneri</i>	72	10
	<i>Hypsiboas albomarginatus</i>	3477	40
Hylidae	<i>Hypsiboas faber</i>	1505	6
	<i>Hypsiboas semilineatus</i>	3176	29
	<i>Itapothyla langsdorffii</i>	3159	8
	<i>Scinax argyreornatus</i>	349	10
	<i>Scinax hayii</i>	452	15
	<i>Scinax littoralis</i>	125	1
	<i>Scinax perereca</i>	124	7
	<i>Scinax perpusillus</i>	1	0
	<i>Scinax trapicheiroi</i>	450	21
	<i>Scinax tymbamirim</i>	1078	78
	<i>Trachycephalus mesophaeus</i>	444	13
Leptodactylidae	<i>Leptodactylus latrans</i>	9272	20
	<i>Physalaemus atlanticus</i>	45	40
	<i>Physalaemus cuvieri</i>	1	0
Microhylidae	<i>Chiasmocleis carvalhoi</i>	9	2
	<i>Elachistocleis bicolor</i>	26	7

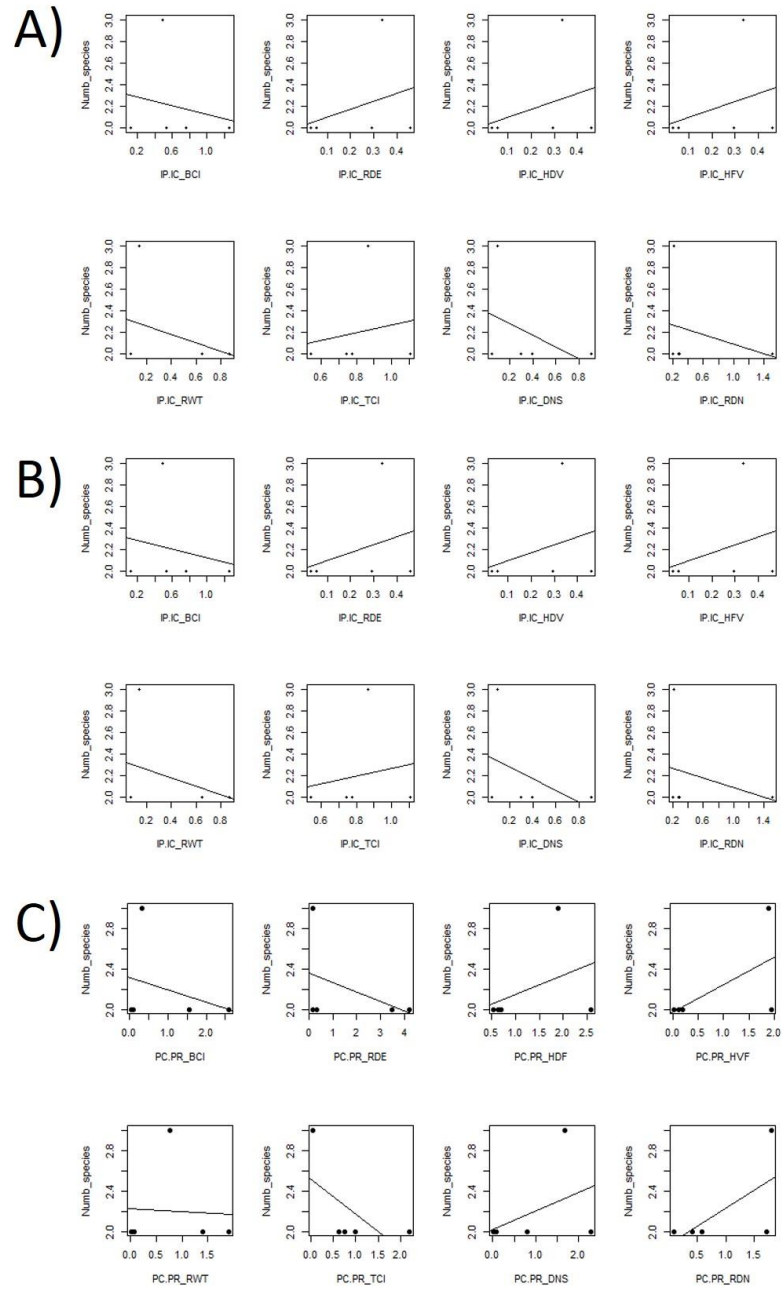


Figure S1: Relationship between T-statistics A) $T_{IP.IC}$, B) $T_{IC.IR}$, and C) $T_{PC.PR}$ and species richness the 21 communities for each tadpole trait.

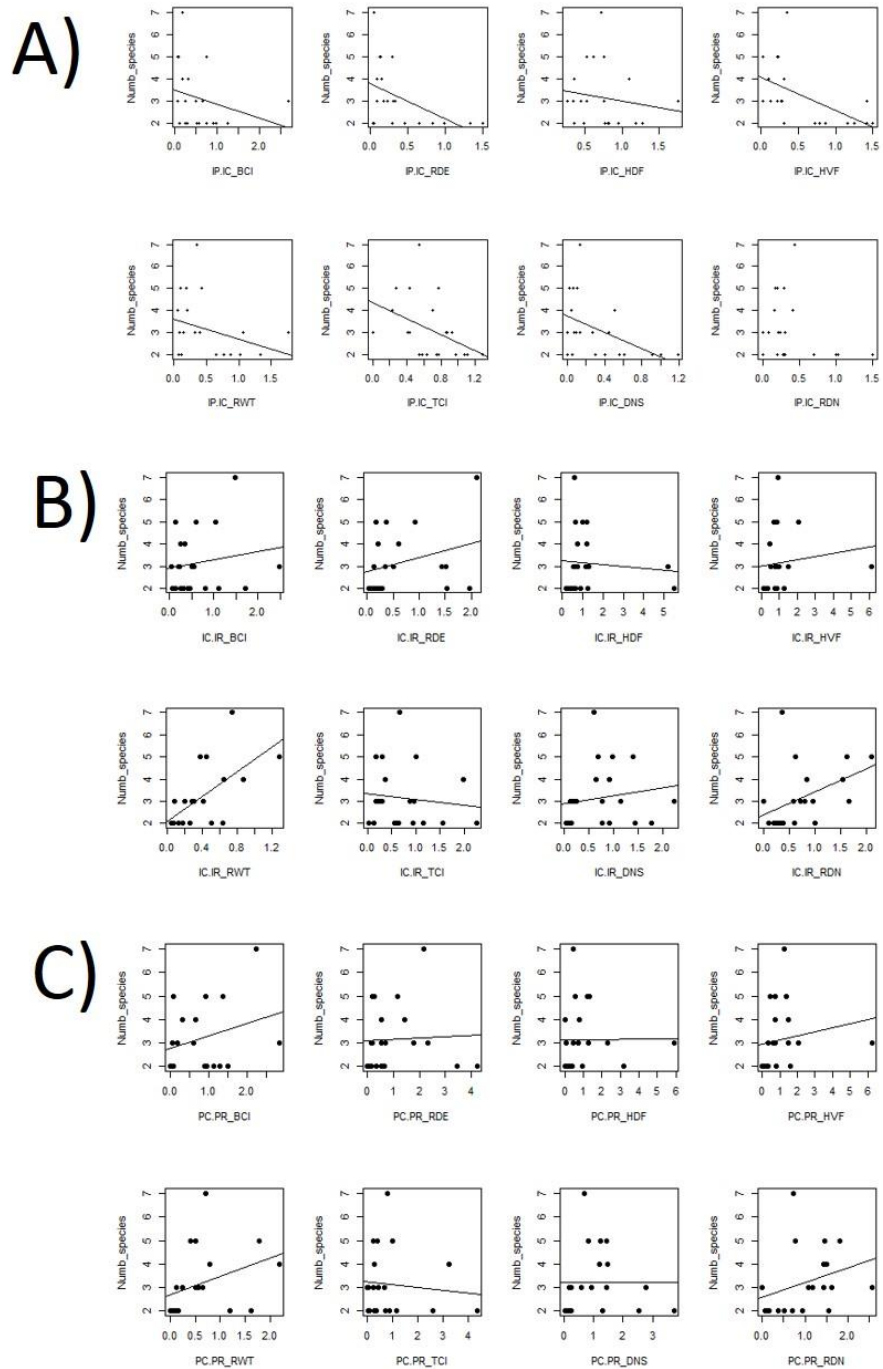


Figure S2: Relationship between T-statistics A) $T_{IP.IC}$, B) $T_{IC.IR}$, and C) $T_{PC.PR}$ and species richness the 21 communities for each tadpole trait.

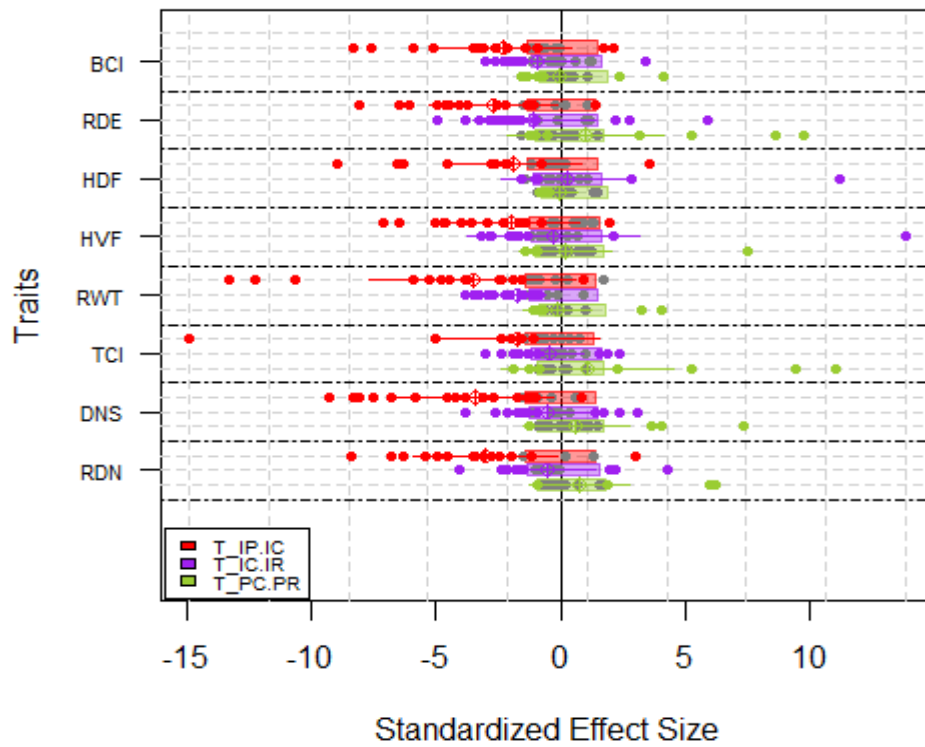


Figure S3: Standardize effect size (SES) of T-statistics for eight functional traits: BCI = Body compression index; RDE = Relative diameter of the eyes; HDF= Relative height of the dorsal fin; HVF = Relative height of the ventral fin; RWT = Relative width of the tail; TCI = Tail compression index; DNS = Distance from nares to snout; RDN = Relative diameter of the nares. The three ratios of variance are: i) $T_{IP.IC}$ – ratio of within population variance to total within community variance; ii) $T_{IC.IR}$ – community-wide variance relative to the total variance in the regional pool; iii) $T_{PC.PR}$ – inter-community variance relative to the total variance in the regional pool. Dot represents the SES values for each community. The crossed circles represent the mean SES values and the segments represent the standard deviation of the SES values. The mean of SES (crossed circles) is significantly different from the null distribution when it is not embedded within the box.

CONSIDERAÇÕES FINAIS

Nossos resultados apresentam novas perspectivas para a compreensão de como os atributos funcionais variam em diferentes tipos de habitat e gradientes ambientais em comunidades de girinos. Também ressaltamos a importância de considerar a influência da variação fenotípica nos atributos de girinos para melhor compreensão da montagem de comunidades e coexistência de espécies.

❖ Os microhabitats de remanso encontrados nos riachos permitem a ocorrência de girinos com morfologia generalizada, promovendo a uma grande similaridade na composição de espécies, riqueza e uniformidade funcional em ambientes lênticos e lóticos.

❖ O tipo de habitat aquático (devido a correnteza nos habitats lóticos) e a porcentagem de cobertura de dossel (devido a diferença nos níveis de produtividade e conseqüentemente disponibilidade de alimento) agem como filtros ecológicos, influenciando a distribuição de atributos funcionais nas comunidades de girinos.

❖ Girinos de habitats lênticos apresentam corpo globoso, focinho comprido, olhos grandes, musculatura caudal estreita, comprimida e mais fina e nadadeiras dorsal e ventral altas. Enquanto que girinos de habitats lóticos possuem corpo deprimido, focinho curto, olhos pequenos, musculatura caudal larga e grossa e nadadeiras dorsal e ventral baixas.

❖ Nossos resultados revelam que além da variabilidade entre as espécies, existe uma variabilidade entre os indivíduos que não deve ser ignorada nos estudos de comunidades de girinos da Amazônia e Mata Atlântica.

❖ A variação intraespecífica ocorreu principalmente em relação à altura da nadadeira dorsal e compressão da cauda. Tais atributos afetam o desempenho dos girinos na natação e apresentam grande plasticidade fenotípica principalmente devido à pressão de predação.

❖ Detectamos baixa sobreposição nos atributos entre as populações em uma comunidade, principalmente em relação ao formato do corpo, tamanho dos olhos e largura da musculatura caudal. Tais atributos afetam a habilidade de forrageamento em diferentes posições na coluna d'água. Enquanto que o tamanho e posição das narinas refletem a habilidade na percepção química relacionada com aquisição de alimentos e detecção de predadores.

❖ Detectamos ação de filtros ecológicos externos às comunidades apenas para a variação intraespecífica na largura da musculatura caudal dos girinos. Isso indica segregação entre girinos de diferentes guildas ecomorfológicas: bentônicos que tem musculatura caudal larga e nectônicos com musculatura caudal estreita.