

TROPICAL TADPOLE ASSEMBLAGES: WHICH FACTORS AFFECT THEIR STRUCTURE AND DISTRIBUTION?

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ABSTRACT

Tropical tadpoles may occur in a range of aquatic habitats, from tree holes (*e.g.*, fitolimns), to permanent ponds and streams. Thus, tadpoles are exposed to a different sort of biotic and abiotic factors, according to the habitat they develop, and these factors may also vary over time. What are these factors? What are their relevance for the distribution of tadpole species and local assemblages? How do they affect the structure of tadpole assemblages? In this review, we explore these questions and recognize some trends regarding the factors influencing tropical tadpole assemblages. We can recognize at least nine major trends regarding the distribution and structure of tropical tadpole assemblages: (1) stream size and microhabitat diversity are important abiotic features influencing species richness and composition; (2) in ponds, the permanence gradient (*e.g.*, hydroperiod), and the heterogeneity of habitat are the main factors modeling tropical tadpole assemblages; (3) species composition seems to be a more relevant assemblage parameter than species richness and should be first considered when planning conservation of both pond and stream-dwelling anurans; (4) predation seems to be the most important biotic interaction structuring tropical tadpole assemblages, with vertebrate predators (*e.g.*, fishes) being more voracious in permanent habitats, while invertebrates (*e.g.*, odonate naiads) are the most important in temporary ones; (5) tadpoles may play a regulatory effect preying upon anuran eggs and recently hatched tadpoles (6) microhabitat use varies in function of breeding habitat choice by adults, presence of predators, phylogeny, stage of development and heterogeneity of the habitat; (7) historical factors restrict the breeding habitats that species may use, and impose behavioral and physiologic constraints; (8) temporal variation in biotic (*e.g.*, risk factors) and abiotic factors (*e.g.*, rainfall distribution), and the reproductive patterns of the species may interfere in the structure of tropical tadpole assemblages, and (9) food resource partitioning in tadpole assemblages may both be or not linked to microhabitat occupation, feeding behavior, and morphology. Future efforts regarding the study of tadpoles should contemplate assemblages associated with streams, and experimental studies.

Keywords: Tadpole assemblage structure; historical factors; biotic factors; habitat structure; microhabitat use.

RESUMO

ASSEMBLEIAS DE GIRINOS TROPICAIS: QUAIS FATORES AFETAM SUA ESTRUTURA E DISTRIBUIÇÃO? Os girinos tropicais ocorrem em uma variedade de habitats aquáticos. Os girinos são expostos a diferentes conjuntos de fatores (bióticos, abióticos), de acordo com o habitat em que vivem, os quais também podem variar temporalmente. Quais são esses fatores? Qual a sua relevância sobre a distribuição das assembleias de girinos? Como eles afetam a sua organização? Nesta revisão, exploramos essas questões e reconhecemos algumas tendências associadas aos fatores que influenciam as assembleias de girinos tropicais. Podemos reconhecer pelo menos nove tendências relacionadas à distribuição e a estrutura de assembleias de girinos: (1) o tamanho dos riachos e a diversidade de microhabitats são importantes características abióticas influenciando a riqueza e a composição de espécies; (2) em poças, o gradiente de permanência (*e.g.*, hidroperíodo) e a heterogeneidade do habitat são os principais fatores moldando as assembleias de girinos; (3) a composição de espécies parece ser um parâmetro das assembleias mais relevante do que a riqueza de espécies e deve ser primeiramente considerado durante o planejamento de ações conservacionistas de anuros associados a poças e riachos; (4) a predação parece ser a interação biótica mais importante na estruturação das assembleias de

girinos, com predadores vertebrados (*e.g.*, peixes) sendo mais vorazes em habitats permanentes e predadores invertebrados (*e.g.*, larvas de odonata) sendo mais vorazes em ambientes temporários; (5) os girinos podem exercer um efeito regulatório, predando ovos e girinos recém eclodidos; (6) o uso do microhabitat varia em função da escolha do habitat reprodutivo pelos adultos, presença de predadores, filogenia, estágio de desenvolvimento e heterogeneidade do habitat; (7) os fatores históricos restringem os habitats reprodutivos que uma espécie utiliza, impondo restrições comportamentais e fisiológicas; (8) a variação temporal nos fatores bióticos (*e.g.*, fatores de risco), abióticos (*e.g.*, distribuição de chuvas), e no padrão de reprodução das espécies pode interferir na estrutura das assembleias de girinos tropicais, e (9) a partição de recursos alimentares em assembleias de girinos podem ou não estar relacionadas ao uso do microhabitat, comportamento reprodutivo e morfologia. Esforços futuros para o estudo de girinos devem contemplar assembleias associadas a riachos, e estudos experimentais.

Palavras-chave: estrutura das assembleias de girinos; fatores históricos; fatores bióticos; fatores abióticos; uso do microhabitat.

AQUATIC BREEDING HABITATS AND RESOURCE PARTITIONING IN TROPICAL TADPOLE ASSEMBLAGES

Most anuran species have a biphasic life cycle and nearly 33% have tadpoles (McDiarmid & Altig 1999). Considering only Brazil, the richest country in the world in terms of amphibians, the number of anuran species with free-swimming larvae increases to nearly 87% (Provetes *et al.* 2012, SBH 2012). Consequently, many species require free water and/or high humidity to develop and metamorphosis. As anurans evolved in the limits of aquatic and terrestrial habitats, natural selection retained a variety of physiological, behavioral, and morphological traits that enable frogs to explore a high diversity of aquatic habitats.

The number of breeding habitats and their distribution are critical factors limiting the occurrence of anuran species (Zimmerman & Bierregaard 1986, Rodrigues *et al.* 2010). In the tropics, anurans breed mainly in lotic (*e.g.*, rivers, creeks and streams) and lentic systems (*e.g.*, ponds, wetlands, tank-bromeliads, wet rocks, water in rock cavities, tree trunks, and inside holes excavated by other animals) (Peixoto 1985, Inger *et al.* 1986, Hödl 1990, Weygoldt & Carvalho-e-Silva 1991, Schiesari 2003, Eterovick & Barata 2006, Moreira *et al.* 2010, Lima *et al.* 2010). These aquatic habitats may vary in their structure (*e.g.*, river width, pond area and depth, canopy cover), limnological characteristics (*e.g.*, conductivity, dissolved oxygen, temperature, lentic, lotic) and hydroperiod (*e.g.*, ephemeral, temporary or permanent habitats), which in turn have different influences on tadpole assemblages (Gascon 1991, Barreto & Moreira 1996, Peltzer & Lajmanovich 2004, Santos *et al.* 2007, Both

et al. 2009, Oliveira & Eterovick 2009, Hawley 2010).

Biotic factors (*e.g.*, predation, competition) can also interfere in assemblage of tadpoles, varying in its extent according to the hydroperiod of habitat (Heyer *et al.* 1975, Hero *et al.* 2001, Fatorelli & Rocha 2008). Permanent habitats present lower risks of desiccation before the end of metamorphosis, but usually allow the occurrence of greater diversity of competitors and predators (Alford 1999). Tadpoles may also have relatively long larval period and acquire larger body sizes in permanent habitats, as they can rely on water level stability and invest in grow (Patterson & McLachlan 1989). On the other hand, the risk of death by desiccation in temporary habitats is relatively high, while predation risk is smaller as temporary habitats tend to hold smaller guild of predators (Heyer *et al.* 1975, Fatorelli & Rocha 2008).

In tadpoles, the main shared resources are space, food and time (Heyer 1973, 1974, Inger *et al.* 1986, Toft 1985, Eterovick & Fernandes 2001, Vasconcelos *et al.* 2011). The breeding aquatic habitat selection by adults, microhabitat use by tadpoles, and temporal variations in assemblage richness and composition respond to a variety of biotic (*e.g.*, predation), abiotic (*e.g.*, stream size, arboreal vegetation cover, microhabitat diversity, salinity) and historical factors (*e.g.*, reproductive modes), as well as to the interactions among them at different scales (*e.g.*, local, regional) (Inger & Voris 1993, Gascon 1995, Zimmerman & Simberloff 1996, Azevedo-Ramos *et al.* 1999, Parris & McCarthy 1999, Hero *et al.* 2001, Smith *et al.* 2007, Oliveira & Eterovick 2009). In this paper we review the key biotic, abiotic, and historical factors known to influence the resource partitioning and, consequently, the structure and distribution of tadpole assemblages in the tropics.

KEY FACTORS

HABITAT STRUCTURE

The structural diversity and availability of breeding habitats are key features to understand the occurrence and distribution of tadpoles (Rossa-Feres & Jim 1994). In tropical streams, structural characteristics of habitat, such as size, marginal vegetation, elevation, water flow, water volume, heterogeneity of microhabitats, dissolved oxygen and conductivity have distinct effects on tadpole assemblages (Odentaal & Bull 1983, Inger *et al.* 1986, Gascon 1991, Inger & Voris 1993, Parris & McCarthy 1999, Richards 2002, Eterovick 2003, Eterovick & Barata 2006, Oliveira & Eterovick 2009).

Studies on tadpole assemblages in tropical streams are still scarce, but these few studies point stream size and heterogeneity of microhabitats as important factors affecting their structure. The stream size in Australia and Madagascar positively affected the number of species (Parris & McCarthy 1999, Strauß *et al.* 2010), while in Brazil the effect was the opposite (Eterovick 2003, Eterovick & Barata 2006). The heterogeneity of microhabitats affected assemblage compositions both in streams of Australia (Parris & McCarthy 1999), in Borneo Island, Indonesia (Inger *et al.* 1986), and in Brazil (Eterovick & Barata 2006), as the pool of species presented different preferences of microhabitat along these gradients of heterogeneity. However, microhabitat heterogeneity did not affect species richness (Inger *et al.* 1986, Parris & McCarthy 1999, Eterovick & Barata 2006). Stream size seems to be a good predictor of assemblage richness, although it plays different roles in rivers from Brazil, Australia and Madagascar. On the other hand, the heterogeneity of microhabitat seems to be a good predictor of assemblage composition, with no relation with species richness at least in Australia (Parris & McCarthy 1999). These generalizations have important implications for tropical amphibian conservation, and suggest that the richness of tadpole assemblages varies in a gradient of stream size, while assemblage composition varies in a gradient of microhabitat heterogeneity. These evidences point that conservation and management efforts of stream-dwelling anurans should consider streams of varied sizes and structurally different (Parris & McCarthy 1999, Eterovick & Barata 2006). Also, species composition may be a more informative parameter for

this aim than species richness, as streams with similar richness may present different species composition (*e.g.* high β -diversity) (Parris & MacCarthy 1999).

Pond habitats are relatively well known and differ from streams mainly to their unpredictability. Characteristics as water temperature, depth, dissolved oxygen, conductivity and presence of vegetation on the shore line and inside ponds are among the main factors affecting pond-dwelling tadpoles in the tropics (Barreto & Moreira 1996, Torres-Orozco *et al.* 2002, Peltzer & Lajmanovich 2004, Muniz *et al.* 2008, Hawley 2009, Moreira *et al.* 2010, Both *et al.* 2011). However, size and hydroperiod are also common features that generally affect the structure of tadpole assemblages (Heyer *et al.* 1975, Santos *et al.* 2007, Fatorelli & Rocha 2008, Both *et al.* 2009).

In terms of species richness, temporary ponds have relatively more tadpole species than semi-permanent or permanent ones (Gascon 1991, Peltzer & Lajmanovich 2004, Both *et al.* 2009). Richness may also correlate with pond size both positively (Peltzer & Lajmanovich 2004), or negatively (Gascon 1991, Moreira *et al.* 2010). The composition of tadpole assemblages in its turn is also related to hydroperiod, and to the heterogeneity of environmental descriptors of ponds (Vasconcelos *et al.* 2009, Moreira *et al.* 2010, Both *et al.* 2011). The heterogeneity of ponds may also correlate with richness and the abundance of individual species (Silva *et al.* 2012). Those gradients of pond size and hydroperiod influence most of the physical-chemical and some biotic variables, as predator composition, and are consequently correlated to pond heterogeneity (Azevedo-Ramos *et al.* 1999). Similarly to stream-dwelling anuran assemblages, some results have shown that species composition may be also a more informative tool in conservation and management of pond-dwelling assemblages than species richness, since species composition is related to environmental heterogeneity, and richer ponds may not present all species from the regional pool (Vasconcelos *et al.* 2009, Moreira *et al.* 2010, Both *et al.* 2011). The conservation planning of anuran pond habitats should consider a range of pond sizes and hydroperiods to ensure a high environmental heterogeneity and the maintenance of the regional pool of species.

There is also the nature of pond bottom, which will determine a faster (such as sandy substrates) or slower drain (as clay substrates), influencing the

hydroperiod and consequently, the development strategy of the species and the survival of tadpoles in ponds (Newman 1992).

BIOTIC FACTORS

Habitat structure is not always associated with tadpole assemblage distribution (*e.g.* Wild 1996, Hero *et al.* 1998, Azevedo-Ramos *et al.* 1999, Eterovick 2003, Vasconcelos & Rossa-Feres 2005, Santos *et al.* 2007). In this context, similar habitats would not have similar assemblages and biotic processes, such as predation and competition, may assume greater relevance in the distribution and structure of these assemblages (*e.g.* Gascon 1991, Azevedo-Ramos *et al.* 1999, Hero *et al.* 1998).

Field studies on competition are rare in tropical tadpoles, and regarding tadpole assemblages competitions does not normally occur in nature (Heyer 1976). There are few evidences that competition is a major force in organizing assemblages because tadpoles are recorded in low densities, or because microhabitat use is only reflecting species-specific preferences of tadpoles (Azevedo-Ramos *et al.* 1999, Eterovick & Sazima 2000, Eterovick & Barros 2003, Eterovick & Barata 2006). However, at least one experimental study in the Brazilian Amazon demonstrated that tadpoles of *Phyllomedusa tomopterna* (Hylidae) reduced growth and survival in the presence of *Osteocephalus taurinus* (Hylidae) (Gascon 1992a). Additionally, in Panama, other experiment showed that *Agalychnis callidryas* (Hylidae) grew 30% faster in the presence of *Dendropsophus ebraccatus* (Hylidae), suggesting that, at least for this pair of species, interspecific competition has relatively larger effects than intraspecific one in the absence of dragonfly larvae predators (Gonzales *et al.* 2011). Competition can be an important force driving tropical assemblages of tadpoles, but we still need more results for a better comprehension of its role.

Predation is a relatively well-studied interaction in tropical tadpoles. Predation effects can be larger than both consumptive and competitive effects (*e.g.* Gonzales *et al.* 2011), and it is suggested to be the key biotic factor acting on stream and pond-dwelling tadpole assemblages, especially in Central Amazon (Heyer *et al.* 1975, Magnusson & Hero 1991, Gascon 1992b, Hero *et al.* 1998, Azevedo-Ramos & Magnusson 1999, Azevedo-Ramos *et al.* 1999, Eterovick & Barata 2006,

Kopp & Eterovick 2006). The risk of predation faced by tadpoles varies with the hydroperiod of the aquatic habitat (Heyer *et al.* 1975, Peltzer & Lajmanovich 2004, Fatorelli & Rocha 2008). Both vertebrate and invertebrate predators restrict tadpole species occurrence through differential predation (*e.g.* Gascon 1992b, Azevedo-Ramos & Magnusson 1999), but permanent habitats, as streams and permanent ponds, present higher water level stability than ephemeral ones, favoring the colonization by fish, and increasing their influence in such habitats (Heyer *et al.* 1975, Hero *et al.* 1998).

Although fish predators can strongly affect the structure of tadpole assemblages (*e.g.* Heyer *et al.* 1975, Hero *et al.* 1998, Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001), tadpole species that are not susceptible to predation by fish demonstrated susceptibility to predation by invertebrates (Azevedo-Ramos & Magnusson 1999). Indeed, microcosm experiments showed that invertebrate predators, such as aeshnid and libelulid naiads, were comparatively more effective than fishes (Gascon 1989, 1992b). Invertebrate predators use to be more common in ponds than fishes, which in turn are more abundant in lotic systems (Gascon 1989, 1992b). Therefore, the assemblages of tadpoles are exposed to a greater diversity of invertebrate predators in temporary than in permanent ponds (Azevedo-Ramos *et al.* 1999, Both *et al.* 2009). In ponds, especially in the temporary ones, invertebrates seem to have a major role as predators and, consequently, on the structure of tadpole assemblages. Tadpoles may also be important predators in ephemeral habitats preying upon eggs and also against new mobile hatchling (Crump 1983, Silva & Juncá 2006, São Pedro *et al.* 2008, Hawley 2009). Cannibalism affects the relative abundance and species composition in ephemeral ponds, and then tadpoles may also play an important role as predator in their assemblages (Hawley 2009).

Different predators have different ecological pressures on their preys. In response, tadpoles adopt different anti-predator strategies. In the presence of dragonfly naiads (which are able to identify the prey only by their movement) tadpoles generally reduce their motility, or present phenotypic plasticity (*e.g.*, behavioral, morphological, and pigmentation changes) to increase survival (Azevedo-Ramos *et al.* 1992, Schmidt & Amézquita 2001, McIntyre *et al.* 2004). The use of microhabitats with aquatic vegetation also

reduces the risk of predation by aquatic insects (Koop *et al.* 2006). Against vertebrate predators (which identify the prey visually, or by its smell), the aposematic coloration and unpalatability can favor tadpoles individually or in group (schooling) (Haddad & D'Heursel 1999). Unpalatability is the primary anti-predator mechanism against fishes, but the use of "free fish" habitats is also an important mechanism of defense for tadpoles (Hero *et al.* 2001).

Predation affects different parameters of tadpole assemblages as their distribution, abundance, richness, and species composition (Hero *et al.* 1998, Azevedo-Ramos & Magnusson 1999, Hero *et al.* 2001). The distribution of predators among aquatic systems promotes a mosaic of available habitats for tadpoles (Hero *et al.* 1998, Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001). This heterogeneity determines which aquatic habitat can be occupied by tadpoles according to the anti-predator mechanism of each species (Azevedo-Ramos & Magnusson 1999, Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001). Thus, the interaction between predator and anti-predator strategies influence the assemblages of tadpoles in two different ways: (1) within the water bodies, since only tadpoles that have the appropriate anti-predator mechanism will survive and (2) among different aquatic habitats, as the heterogeneous distribution of predators result in a mosaic of available habitats that interact with a variety of anti-predator defenses exhibited by tadpoles (Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001).

The relationships between tadpoles and biotic characteristics of aquatic habitats (*e.g.*, predator-prey interaction) are so complex that prevent us to recognize a single most relevant biotic factor influencing tadpole assemblages. In fact, the aquatic habitats used by tadpoles are usually so variable that, depending on the circumstances, as hydroperiod, one or other factor may be determinant to structure local assemblages. Fishes are known to be important predators in streams and permanent habitats (*e.g.* Heyer *et al.* 1975, Hero *et al.* 1998, Azevedo-Ramos & Magnusson 1999, Hero *et al.* 2001), while invertebrate predators, as odonate naiads, play a major role in ponds and temporary habitats (*e.g.* Gascon 1992b, Azevedo-Ramos & Magnusson 1999). Cannibalism is common among tadpoles which make tadpoles also important predators in ephemeral habitats (Crump 1983, Hawley 2009). In the absence of predators, priority effects and

competition may assume more relevance in tadpole assemblage structure (Gonzales *et al.* 2011). Which kind of interactions are more prone to affect tadpole assemblages in each particular conditions, will depend on the set of structural components of the habitat.

MICROHABITAT USE

In stable habitats, with comparatively lower effects of seasonality, space is the primary resource shared by tadpoles, making the microhabitat availability an important cue to understand its use (Heyer 1973, 1974, Inger *et al.* 1986). The coexistence among different species within a particular water body depends in part on the differential use of available microhabitats (Cardoso *et al.* 1989, Eterovick & Barata 2006). In this context, the spatial heterogeneity is important to explain the coexistence of tadpoles sharing a particular habitat (Rossa-Feres & Jim 1994).

Tadpoles can occupy a variety of microhabitats and exhibit a high plasticity in their use (Eterovick & Barros 2003, Eterovick *et al.* 2010a, 2010b, Fatorelli *et al.* 2010). Tadpoles mainly differ in position in water column, mean depth, and type of substrate (Cardoso *et al.* 1989, Hero 1990, Eterovick & Fernandes 2001, Kopp & Eterovick 2006, Kopp *et al.* 2006, Prado *et al.* 2009). These differences in microhabitat use may result from the influence of factors such as differences in evolutionary history (*e.g.*, Eterovick & Fernandes 2001), interactions among tadpoles of different species, distinct cohorts, body size and stage of development (*e.g.*, Wild 1996), and environmental pressures (*e.g.*, Kopp *et al.* 2006).

The microhabitat availability to tadpoles depends, in a large extent, on the oviposition site used by adult anurans and the presence of potential predators (Murphy 2003, Kopp *et al.* 2006, Eterovick & Ferreira 2008). Adults can assess the risks will be faced by tadpoles avoiding habitats with high predators densities and high desiccation risks, limiting the microhabitats that will be available (Murphy 2003). The presence of predators may also influence the microhabitat preference of tadpoles, favoring the use of sheltered microhabitats, restricting microhabitats that could be used by tadpoles (Kopp *et al.* 2006). Additionally, morphology, feeding behavior (ecomorphological guilds *sensu* Altig & Johnston 1989), and phylogeny also interfere in microhabitat selection by tadpoles, since these features can be more effective in different microhabitats, imposing a strong historical

component to allow their use, although it varies among taxonomic groups (Inger *et al.* 1986, Eterovick & Fernandes 2001).

Tadpoles may also have different degrees of preference in microhabitat use according with the habitat capacity to retain water. In unpredictable habitats, where large variations in the hydrological cycle take place, microhabitat specialization becomes disadvantageous and assemblages with generalist species are usually selected (Eterovick & Barros 2003). On the other hand, predictable habitats may exhibit species very selective in terms of microhabitat use, affecting the composition of assemblages from water bodies that differ in microhabitat availability (Inger *et al.* 1986, Eterovick & Barata 2006). Thus, the interference that microhabitat availability and its use have on the structure of tadpole assemblages greatly depends on water stability of the aquatic habitat.

CAN WE IDENTIFY A KEY HISTORICAL FACTOR?

Tadpole assemblages responses cannot always be clearly associated with neither abiotic or biotic factors, which result in an apparent lack of trends or patterns, and could led one to believe that their organization result by chance (Heyer 1973, Gascon 1991, Eterovick & Barros 2003, Eterovick 2003). It is important to understand how habitat heterogeneity and biotic interactions affect the occupation of water bodies by tadpoles, but considering only these features is not enough.

Historical factors contribute to the distribution and diversity of amphibians on a global scale (Buckley & Jetz 2007). Similarly, the occupation of aquatic habitats by tadpoles also depends primarily on historical constraints imposed by colonization and phylogeny of species (Gascon 1991, Zimmerman & Simberloff 1996). An example of the role of historical factors acting on the distribution of amphibians is the high diversity of reproductive modes they exhibit, the largest among tetrapods (Haddad & Prado 2005).

The reproductive mode of anurans is defined by the combination of characters including the site and microhabitat of oviposition, eggs and characteristics of spawning, length of development, stage and size of hatches and type of parental care, if present (Salthe & Duellman 1973). Reproductive modes present a higher diversification for lentic habitats (*e.g.*, Box 1. Haddad & Prado 2005), a phylogenetic signature and reflect the species dependence on a set of

characteristics related to reproductive and developmental habitat, directly interfering in water body selection by adults (Duellman 1989, Zimmerman & Simberloff 1996). As tadpoles of most species lack adaptations that prevent them to develop in fast running waters, still water bodies tend to present richer tadpole assemblages than streams, at least in lowland areas (*e.g.* Gascon 1991). On the other hand, mountain areas may present more species and reproductive modes associated to streams, as the retention of still water bodies may be difficult in geographically irregular areas (Inger 1966, Duellman 1988). So, to understand the distribution of tadpole assemblages among aquatic habitats we need to consider the geography and the heterogeneity of the reproductive habitats coupled with the reproductive modes that occur in a particular area (Zimmerman & Bierregaard 1986, Zimmerman & Simberloff 1996, Vasconcelos *et al.* 2009, Both *et al.* 2011). Because of the interdependence between reproductive mode of anurans, geography, and particular features of breeding habitats, a prior knowledge of the reproductive mode of the assemblages may contribute to anuran conservation actions when selecting the appropriate habitats that cover the set of species occurring in an area (*e.g.*, environments richer in lentic, lotic, or both habitats).

The physiological ability of tadpoles to survive in the absence of free water is another important aspect related to historical factors. Most temporary habitats face periods of desiccation, and until the next income of rainwater, the only source of moisture is that retained on leaves or mud accumulated on the bottom of the dried pond. In this case, tadpoles that were developing depend on their ability to survive in the absence of free water that is inherent to the species (Newman 1992). Apparently, this variation in physiological capacity is, in part, a function of the habitat in which tadpoles have evolved (*e.g.*, rate of consumption of dissolved oxygen, which may reflect their susceptibility to its lack), mass, and body size (*e.g.*, larger and heavy tadpoles tend to survive for longer periods) (Fatorelli 2011). However, there are few studies and experiments in the tropics to understand the differences in survival abilities of different tadpole species to the absence of free water (*e.g.*, Fatorelli 2011).

TEMPORAL VARIATIONS

Time (*e.g.* seasonal variations) was first considered as the most important dimension partitioned

by tadpoles (Toft 1985). Factors influencing the structure and distribution of tadpole assemblages may vary over time. Tadpoles from distinct species differ in their occurrence periods along the year and the richness of an assemblage can be related to the temporal variation of environmental parameters (Eterovick & Sazima 2000, Eterovick & Fernandes 2001, Both *et al.* 2009, Moreira *et al.* 2010).

In anurans, the time refers to changes that may occur in assemblages in response to rainfall and breeding habitats availability, different use according to the temporal reproductive strategy, phenology of species, and activity and breeding site choice by adults (Crump 1974, Gascon 1992a, Murphy 2003, Gottsberger & Gruber 2004, Boquimpani-Freitas *et al.* 2007). These features have evolved in past climate conditions, but they actually respond to present biotic (*e.g.*, predation risk) and abiotic factors (*e.g.*, rainfall distribution, air humidity, temperature, photoperiod and/or light intensity, hydroperiod) (Aichinger 1987, Hatano *et al.* 2002, Murphy 2003, Van Sluys *et al.* 2006, Almeida-Gomes *et al.* 2007, Fatorelli *et al.* 2010). Consequently, the temporal distribution of tadpole assemblages and their occupation strategies are related to factors that affect the reproductive attributes of adults.

Rainfall has been shown to be the main abiotic factor regulating temporal reproductive activity of anurans associated to both temporary (*e.g.*, ponds) and permanent habitats (*e.g.*, streams) (Heyer 1973, Rico *et al.* 2004, Boquimpani-Freitas *et al.* 2007, Vasconcelos *et al.* 2011). The breeding habitats available for anurans may interfere on the reproductive period of species and consequently on the period of tadpole occurrence. In temporary habitats, the temporal variation of rainfalls strongly affects the hydroperiod and the availability of habitats (Heyer 1973). In these environments the richness and abundance of tadpoles tend to be affected by water availability and rainfall (Eterovic & Sazima 2000, Both *et al.* 2009, Vasconcelos *et al.* 2011, Moreira *et al.* 2010). For streams, which have relatively more stable water levels, it has not being possible to recognize any trend regarding rainfall and the parameters of assemblages. However, in streams, some tadpoles may present relatively constant abundances year around (Almeida-Gomes 2012, Borges-Júnior 2007, Leite *et al.* 2008, Fatorelli *et al.* 2010), or even higher abundances in the dry period, supposedly as an adaptation to complete the metamorphose in the rainiest

period (Eterovick *et al.* 2010a). These few evidences suggest that in streams the richness and abundance of tadpoles show relatively less temporal fluctuations.

The temporal reproductive strategies of anurans can be distinguished based on their annual reproductive activity, being classified as continuous, prolonged or explosive (Crump 1974). Explosive breeder species, as *Itapotihyla langsdorffii* (Hylidae), are usually associated with ephemeral habitats, such as temporary ponds (*e.g.* Vrcibradic *et al.* 2009), while species that reproduce for long periods (continuous breeders) as *Scinax trapicheiroi*, *Aplastodiscus eugenioi*, and *Phasmahyla jandaia* (all Hylidae), and prolonged breeders as *Crossodactylus aeneus* (Hylodidae) and *Proceratophrys tupinamba* (Cycloramphidae) may show some preference for more predictable habitats such as streams and permanent ponds (Crump 1974, Rico *et al.* 2004, Almeida-Gomes 2012, Borges-Júnior 2007, Leite *et al.* 2008, Fatorelli *et al.* 2010). The same species may also present different temporal reproductive pattern. For example, different populations of *Scinax rizibilis* may present explosive reproduction (Pombal & Haddad 2005), or more prolonged temporal pattern (Pombal 1997). These strategies are usually associated with the availability of reproductive habitat (temporary or permanent habitats) and, as discussed above, it influences which period of the year a tadpole species may occur in an assemblage.

The reproductive phenology of anurans is the period of adult reproductive activity. Adult reproductive phenology can favor early breeding species through priority effects. For particular species, larger tadpoles from cohorts that first colonized the water body may have advantages over younger cohorts, negatively affecting their fitness (*e.g.*, growth rate, survival) (Gascon 1989, 1992a, Gonzales *et al.* 2011). So, priority effects, and consequently adult reproductive phenology can directly interfere in tadpole assemblages since those species that primarily colonized the aquatic habitat are favored and represent potential sources of risk for late breeders.

The breeding habitat selection by adults directly affects tadpoles that will occur and can present a strong temporal component. Reproductive modes may interfere in the breeding habitat selection, but risk factors can also affect this selection and present a strong temporal component. *Edalorhina perezii*, a Neotropical frog from Peru, avoided pools with predator, and females also avoided pools with conspecific tadpoles (Murphy 2003). Also, female sensitivity to predators

decrease in the late season, indicating that risk factors may impose changes in the habitat selection for reproduction that vary temporally (Murphy 2003).

FOOD RESOURCE PARTITIONING

The relevance of food resource partitioning in tadpole assemblages remains unclear. Space and time are usually pointed as more important than food partitioning (Heyer 1974, Toft 1985). For this point of view, differences in food resources may not contribute more than patterns of occurrence, neither microhabitat use to characterize niches occupied by tadpoles (Heyer 1973, Heyer 1974, Prado *et al.* 2009). These means that tadpoles may occur at different time periods and use space differently in a pond, despite show no differences in food selected (*e.g.* Heyer 1973). On the other hand, feeding behavior of tadpoles may be partially coupled with morphology and microhabitat distribution resulting in differences in diet composition, which contribute with food partitioning (Inger 1986, Rossa-Feres *et al.* 2004, Escheverría *et al.* 2007, Souza Filho *et al.* 2007).

Works on food resource partitioning in tropical tadpole assemblages are still scarce and they are restricted to pond-dwelling tadpoles. The available data suggests that relevance of food partitioning on tadpole assemblages varies differently in these habitats, and it may results from the interaction of several factors (*e.g.* Heyer 1973, Rossa-Feres *et al.* 2004).

FINAL CONSIDERATIONS

We can recognize at least nine major trends regarding the distribution and structure of assemblages of tropical tadpoles: (1) stream size and microhabitat diversity are important abiotic features influencing species richness and composition in assemblages of tropical tadpoles; (2) in ponds, the permanence gradient (*e.g.*, hydroperiod), and the heterogeneity of habitat are the main factor modeling tropical tadpole assemblages in lentic systems; (3) species composition seems to be a more relevant assemblage parameter than species richness and should be first considered when planning conservation of both pond and stream-dwelling anurans; (4) predation seems to be the most important biotic interaction structuring tropical tadpole assemblages, with vertebrate predators (*e.g.*, fishes) being more voracious in permanent habitats, while invertebrates (*e.g.*, odonate naiads) are the most important in temporary ones; (5)

tadpoles may play a regulatory effect preying upon anuran eggs and recently hatched tadpoles (6) microhabitat use varies in function of breeding habitat choice by adults, presence of predators, phylogeny, stage of development and heterogeneity of the habitat; (7) historical factors restrict the breeding habitats that a species may use, and impose behavioral and physiologic constrains; (8) temporal variation in biotic (*e.g.*, risk factors) and abiotic factors (*e.g.*, rainfall distribution), and the reproductive patterns of the species may interfere in the structure of tropical tadpole assemblages, and (9) food resource partitioning in tadpole assemblages may both be or not linked to microhabitat occupation, feeding behavior, and morphology.

Much effort in diverse areas must be done to accomplish a reasonable knowledge on which factors and how they affect structure and distribution of tropical tadpole assemblages. Future endeavors should contemplate assemblage of tadpoles associated with streams, which are relatively understudied compared with those of pond-dwelling tadpoles. Competition interactions among tadpoles are still not well understood, and must be more deeply investigated. These efforts should contemplate experimental approaches in both micro and mesocosm scales. To understand how a species that first colonize a free tadpole habitat affect the subsequent species is essential to the comprehension of assemblage structure. This approach is important especially in seasonal habitats, where temporal partitioning has been showed to be less important in structuring tadpole assemblages. Temporal partitioning through priority effects may have an important role in structuring tadpole assemblages in these environments. Studies on feeding habitats and food partitioning in tadpoles are also needed, as they are still scarce in the literature. These studies should take into account not only the food contents of tadpoles, but also their availability in the habitat. Finally, we strongly recommend as a first step tool to the specific identification of tadpoles, the work done by Provetes *et al.* (2012) that brings a compilation of the references of the description of tadpoles from Brazil.

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REFERENCES

- AICHINGER, M. 1987. Annual activity patterns of anurans in seasonal neotropical environment. *Oecologia*, 71: 583-592. <http://dx.doi.org/10.1007/BF00379302>.
- ALFORD, R.A. 1999. Ecology: Resource use, competition and predation. Pp. 240-278. In: R.W. McDiarmid & R. Altig (eds.). Tadpoles. The biology of anuran larvae. The University of Chicago Press, Chicago and London. 444p.
- ALMEIDA-GOMES, M.; LAIA, R.C.; HATANO, F.H.; VAN SLUYS, M. & ROCHA, C.F.D. 2012 Population dynamics of tadpoles of *Crossodactylus gaudichaudii* (Anura: Hylodidae) in the Atlantic Rainforest of Ilha Grande, southeastern Brazil *Journal of Natural History*, 46: 2725-2733. <http://dx.doi.org/10.1080/00222933.2012.717643>.
- ALMEIDA-GOMES, M.; VAN SLUYS, M. & ROCHA, C.F.D. 2007. Calling activity of *Crossodactylus aeneus* (Anura: Hylodidae) in an Atlantic Rainforest area at Ilha Grande, Rio de Janeiro, Brazil. *Belgian Journal of Zoology*, 137: 203-207.
- ALTIG, R. & JOHNSTON, G.F. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs*, 3: 81-109.
- AZEVEDO-RAMOS, C.; VAN SLUYS, M.; HERO, J.M. & MAGNUSSON, W.E. 1992. Influence of tadpole movement on predation by Odonata naiads. *Journal of Herpetology*, 26: 335-338.
- AZEVEDO-RAMOS, C.B.A. & MAGNUSSON W.E. 1999. Tropical tadpole vulnerability to predation: association between laboratory results and prey distribution in an Amazonian Savanna. *Copeia*, 1999: 58-67.
- AZEVEDO-RAMOS, C.; MAGNUSSON, W.E. & BAYLISS, P. 1999. Predation as the key factor structuring tadpole assemblages in a savanna area in central Amazonia. *Copeia*, 1999: 22-33.
- BARRETO, L. & MOREIRA, G. 1996. Seasonal variation in age structure and spatial distribution of a Savanna larval anuran assemblage in central Brazil. *Journal of Herpetology*, 30: 87-92.
- BOQUIMPANI-FREITAS, L.; MARRA, R.V.; VAN SLUYS, M. & ROCHA C.F.D. 2007. Temporal niche of acoustic activity in anurans: interspecific and seasonal variation in a neotropical assemblage from south-eastern Brazil. *Amphibia-Reptilia*, 28: 269-276. <http://dx.doi.org/10.1163/156853807780202422>.
- BORGES-JÚNIOR, V.N.T. 2007. Ecologia de girinos e adultos de *Aplastodiscus eugenioi* (Anura: Hylidae) na Mata Atlântica da Ilha Grande, Angra dos Reis, RJ. *Dissertação de Mestrado*, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brasil. 104p.
- BOTH, C.; SOLÉ, M.; SANTOS, T.G. & CECHIN, S.Z. 2009. The role of spatial and temporal descriptors for Neotropical tadpole communities in southern Brazil. *Hydrobiologia*, 624:125-13. <http://dx.doi.org/10.1007/s10750-008-9685-5>.
- BOTH, C.; CECHIN, S.; MELO, A.S. & HARTZ, S.M. 2011. What control tadpole richness and guild composition in ponds in subtropical grasslands? *Austral Ecology*, 36: 530-536. <http://dx.doi.org/10.1111/j.1442-9993.2010.02183>.
- BUCKLEY, L.B. & JETZ, W. 2007. Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B*, 274: 1167-1173. <http://dx.doi.org/10.1098/rspb.2006.0436>.
- CARDOSO, A.J; ANDRADE, G.V. & HADDAD, C.F.B. 1989. Distribuição espacial em comunidades de anfíbios (Anura) no Sudeste do Brasil. *Revista Brasileira de Biologia*, 49: 241-249.
- CRUMP, M.L. 1974. Reproductive strategies in a tropical anuran community. *University of Kansas, Museum of Natural History. Miscellaneous Publications*, 61:1-68.
- CRUMP, M.L. 1983. Opportunistic cannibalism by amphibian larvae in temporary aquatic environments. *The American Naturalist*, 121: 281-289.
- DUELLMAN, W.E. 1988. Patterns of species diversity in anuran amphibians in the American tropics. *Annals of the Missouri Botanical Garden*, 75: 79-104.
- DUELLMAN, W.E. 1989. Alternative life-history styles in anuran amphibians: evolutionary and ecological implications. Pp. 101-126. In: M.N Burton (ed.). Alternative life-history styles of animals. Academic Publisher, Dordrecht. 617p.
- ESCHEVERRÍA, D.D.; VOLPEDO, A.V. & MASCITI, V.I. 2007. Diet of tadpoles from a pond in Iguazu National Park, Argentina. *Gayana*, 71: 8-14. <http://dx.doi.org/10.4067/S0717-65382007000100002>.
- ETEROVICK, P.C. & SAZIMA, I. 2000. Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. *Amphibia-Reptilia*, 21: 439-461.
- ETEROVICK, P.C. & FERNANDES, G.W. 2001. Tadpole distribution within montane meadow streams at the Serra do Cipó, south-eastern Brazil: ecological or phylogenetic constraints? *Journal of Tropical Ecology*, 17: 683-693. <http://dx.doi.org/10.1017/S026646740100150>.
- ETEROVICK, P.C. 2003. Distribution of anuran species among mountain streams in south-eastern Brazil. *Journal of Tropical Ecology*, 19: 219-228. <http://dx.doi.org/10.1017/S0266467403003250>.
- ETEROVICK, P.C. & BARROS, I.S. 2003. Niche occupancy in South eastern Brazilian tadpole communities in montane-meadow streams. *Journal of Tropical Ecology*, 19: 439- 448. <http://dx.doi.org/10.1017/S026646740300347>.
- ETEROVICK, P.C. & BARATA, I.M. 2006. Distribution of tadpoles within and among Brazilian streams: the influence of predator, habitat size and heterogeneity. *Herpetologica*, 62: 365-377. <http://dx.doi.org/10.1655/0018-0831>.

- ETEROVICK, P.C. & FERREIRA, A.D.M. 2008. Breeding habitat and microhabitat choice by male and female frogs: are there differences between sexes and seasons? *Herpetologica*, 64: 397-405. 1 <http://dx.doi.org/0.1655/08-025R1.1> .
- ETEROVICK, P.C.; LAZAROTTI, I.; FRANCO, B.P. & DIAS, C.J. 2010a. Seasonal variation of tadpole spatial niches in permanent streams: the role of predation risk and microhabitat availability. *Austral Ecology*, 35: 879-887. <http://dx.doi.org/10.1111/j.1442-9993.2009.02094> .
- ETEROVICK, P.C.; RIEVERS, C.R.; KOPP, K.; WACHLEVSKI, M.; FRANCO, B.P.; DIAS, C.J.; BARATA, I.M.; FERREIRA, A.D.M. & AFONSO, L.G. 2010b. Lack of phylogenetic signal in the variation in anuran microhabitat use in southeastern Brazil. *Evolutionary Ecology*, 24: 1-24. <http://dx.doi.org/10.1007/s10682-008-9286-9> .
- FATORELLI, P.C. & ROCHA, C.F.D. 2008. O que molda a distribuição das guildas de girinos tropicais? Quarenta anos de busca por padrões. *Oecologia brasiliensis*, 12: 733-742. <http://dx.doi.org/10.4257/141> .
- FATORELLI, P.; COSTA, P.N.; LAIA, R.C.; ALMEIDA-SANTOS, M.; VAN SLUYS, M. & ROCHA, C.F.D. 2010. Description, microhabitat and temporal distribution of the tadpoles of *Proceratophrys tupinamba* Prado and Pombal, 2008. *Zootaxa*, 2684: 57-62.
- FATORELLI, P.C. 2011. Ocorrência e distribuição espacial e temporal das larvas de anuros (Amphibia) em diferentes sistemas aquáticos da Ilha Grande (Rio de Janeiro). *Tese de Doutorado*. Universidade do Estado do Rio de Janeiro, Rio de Janeiro, RJ, Brasil. 163p.
- GASCON, C. 1989. Predator-prey size interactions in tropical ponds. *Revista Brasileira de Zoologia*, 6: 701-706.
- GASCON, C. 1991. Population- and community-level analyses of species occurrences of Central Amazonian rainforest tadpoles. *Ecology*, 72: 1731-1746. <http://dx.doi.org/10.2307/1940972> .
- GASCON, C. 1992a. The effects of reproductive phenology on larval performance traits in a three-species assemblage of Central Amazonian tadpole. *Oikos*, 65: 307-313.
- GASCON, C. 1992b. Aquatic predators and tadpole prey in Central Amazonia: field data and experimental manipulations. *Ecology*, 73: 971-980. <http://dx.doi.org/10.2307/1940173> .
- GASCON, C. 1995. Tropical larval anuran fitness in the absence of direct effects of predation and competition. *Ecology*, 76: 2222-2229. <http://dx.doi.org/10.2307/1941695> .
- GONZALES, S.C.; TOUCHON, J.C. & VONESH, J.R. 2011. Interactions between competition and predation shape early growth and survival of two neotropical Hylidae tadpoles. *Biotropica*, 43: 633-639. <http://dx.doi.org/10.1111/j.1744-7429.2010.00748> .
- GOTTSBERGER, B. & GRUBER, E. 2004. Temporal partitioning of reproductive activity in a neotropical anuran community. *Journal of Tropical Ecology*, 20: 271-280. <http://dx.doi.org/10.1017/S0266467403001172> .
- HADDAD, C.F.B. & D'HEURSEL, A. 1999. Unpalatability of *Hyla semilineata* tadpoles (Anura) to captive and free ranging vertebrates predators. *Ethology Ecology & Evolution*, 11: 339-348. <http://dx.doi.org/10.1080/08927014.1999.9522818> .
- HADDAD, C.F.B. & PRADO, C.P.A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil. *Bioscience*, 55: 207-217. <http://dx.doi.org/10.1641/0006-3568> .
- HATANO, F.H.; ROCHA, C.F.D. & VAN SLUYS, M. 2002. Environmental factors affecting calling activity of tropical diurnal frog *Hylodes phyllodes* (Anura: Leptodactylidae). *Journal of Herpetology*, 36: 314-318. <http://dx.doi.org/10.1670/0022-1511> .
- HAWLEY, T.J. 2009. The ecological significance and incidence of intraguild predation and cannibalism among anurans in ephemeral tropical pools. *Copeia*, 2009: 748-757. <http://dx.doi.org/10.1643/CP-08-114> .
- HAWLEY, T.J. 2010. Influence of forest cover on tadpole vital rates in two tropical treefrogs. *Herpetological Conservation and Biology*, 5: 233-240.
- HERO, J.M. 1990. An illustrated key to tadpoles occurring in the Central Amazon rainforest, Manaus, Amazonas, Brazil. *Amazonia*, 9: 201-262.
- HERO, J.M.; GASCON, C. & MAGNUSSON, W.E. 1998. Direct and indirect effects of predation on tadpole community structure in the Amazon rain forest. *Australian Journal of Ecology*, 23: 474-482. <http://dx.doi.org/10.1111/j.1442-9993.1998.tb00755> .
- HERO, J.M.; MAGNUSSON, W.E.; ROCHA, C.F.D. & CATTERALL, C.P. 2001. Anti-predator defense influence the distribution of amphibian prey species in the Central Amazon rain forest. *Biotropica*, 33: 131-141. <http://dx.doi.org/10.1111/j.1744-7429.2001.tb00163> .
- HEYER, W.R. 1973. Ecological interactions of frog larvae at a seasonal tropical location in Thailand. *Journal of Herpetology*, 7: 337-361.
- HEYER, W.R. 1974. Niche measurements of frog larvae from a seasonal tropical location in Thailand. *Ecology*, 55: 651-656. <http://dx.doi.org/10.2307/1935156> .
- HEYER, W.R.; MCDIARMID, R.W. & WEIGMANN, D.L. 1975. Tadpoles, predation, and pond habitats in the tropics. *Biotropica*, 7: 100-111.
- HEYER, W.R. 1976. Studies in larval amphibian habitat partitioning. *Smithsonian Contributions to Zoology*, 242: 1-27.
- HÖDL, W. 1990. Reproductive diversity in Amazonian lowland frogs. *Fortschritte der Zoologie*, 38: 41-60.
- INGER, R.F. The systematics and zoogeography of the amphibian of Borneo. *Fieldiana: Zoology*, 52: 1-402.
- INGER, R.F. 1986. Diet of tadpoles living in a Bornean rain Forest. *Atyles*, 5: 153-164.
- INGER, R.F.; VORIS, H.K. & FROGNER, K.J. 1986. Organization of a community of tadpoles in rain forest streams in

- Borneo. *Journal of Tropical Ecology*, 2: 193-205. <http://dx.doi.org/10.1017/S026646740000808> .
- INGER, R.F. & VORIS, H.K. 1993. A comparison of amphibian communities through time and from place to place in Bornean forests. *Journal of Tropical Ecology*, 9: 409-433. <http://dx.doi.org/10.1017/S0266467400007483> .
- KOPP, K. & ETEROVICK, P.C. 2006. Factors influencing spatial and temporal structure of frog assemblages at ponds in south eastern Brazil. *Journal of Natural History*, 40: 1813-1830. <http://dx.doi.org/10.1080/00222930601017403> .
- KOPP, K.; WACHLEVSKI, M. & ETEROVICK, P.C. 2006. Environmental complexity reduces tadpole predation by water bugs. *Canadian Journal of Zoology*, 84: 136-140. <http://dx.doi.org/10.1139/Z05-186> .
- LEITE, F.S.F.; PACHECO, B.G. & ETEROVICK, P.C. 2008. Development and demography of *Phasmahyla jandaia* (Bokermann and Sazima, 1978) tadpoles in an Atlantic Forest site, southeastern Brazil. *Journal of Natural History*, 42: 2777-2791. <http://dx.doi.org/10.1080/00222930802361022> .
- LIMA, A.M.X.; GAREY, M.V.; NOLETO, R.B. & VERDADE, V.K. 2010. Natural history of the Lutz's frog *Cycloramphus lutzorum* Heyer, 1983 (Anura: Cycloramphidae) in the Brazilian Atlantic Forest: description of the advertisement call, tadpole, and karyotype. *Journal of Herpetology*, 44: 360-371. <http://dx.doi.org/10.1670/08-185.1> .
- MACDIAMIRD, R.W. & ALTIG, R. 1999. *Tadpole. The Biology of anuran larvae*. First Edition. The University of Chicago Press, Chicago and London. 444p.
- MAGNUSSON, W.E. & HERO, J.M. 1991. Predation and the evolution of complex oviposition behavior in Amazon rainforest frogs. *Oecologia*, 86: 310-318. <http://dx.doi.org/10.1007/BF00317595> .
- McINTYRE, P.B.; BALDWIN, S. & FLECKER, A.S. 2004. Effects of behavioral and morphological plasticity on risk of predation in a Neotropical tadpole. *Oecologia*, 141: 130-138. <http://dx.doi.org/10.1007/s00442-004-1652> .
- MOREIRA, L.F.B.; MACHADO, I.F.; GARCIA, T.V. & MALTCHIK, L. 2010. Factors influencing anuran distribution in coastal dune wetlands in southern Brazil. *Journal of Natural History*, 44: 1493-1507. <http://dx.doi.org/10.1080/00222931003632690> .
- MUNIZ, K.P.R.; GIARETTA, A.A.; SILVA, W.R. & FACURE, K.G. 2008. Auto ecologia de *Hypsiboas albopunctatus* (Anura, Hylidae) em área de Cerrado no sudeste do Brasil. *Iheringia*, 98: 254-259. <http://dx.doi.org/10.1590/S0073-47212008000200014> .
- MURPHY, P.J. 2003. Context-dependent reproductive site choice in a neotropical frog. *Behavioral Ecology*, 14: 626-633. <http://dx.doi.org/10.1093/beheco/arg042> .
- NEWMAN, R.A. 1992. Adaptive plasticity in amphibian metamorphosis. *Biosciences*, 42: 671-678.
- ODENTAAL, F.J. & BULL, C.M. 1983. Water movements, tadpoles competitions and limits to the distribution of the frogs *Ranidella riparia* and *R. signifera*. *Oecologia*, 57: 361-367. <http://dx.doi.org/10.1007/BF00377181> .
- OLIVEIRA, F.F.R. & ETEROVICK P.C. 2009. The role of river longitudinal gradients, local and regional attributes in shaping frog assemblages. *Acta Oecologica*, 35: 727-738.
- PARRIS, K.M. & MCCARTHY, M.A. 1999. What influences the structure of frogs assemblages at forest streams? *Australian Journal of Ecology*, 24: 495-502. <http://dx.doi.org/10.1046/j.1442-9993.1999.00989> .
- PATTERSON, J.W. & MCLACHLAN, A.J. 1989. Larval habitat duration and size at metamorphosis in frogs. *Hydrobiologia*, 171: 121-126. <http://dx.doi.org/10.1007/BF00008172> .
- PEIXOTO, O.L. 1995. Associação de anuros a bromeliáceas na Mata Atlântica. *Revista da Universidade Rural, Série Ciências da Vida*, 17: 75-83.
- PRADO, V.H.M.; FONSECA, M.G.; ALMEIDA, F.V.R.; NECCHI, O.JR. & ROSSA-FERES, D.C. 2009. Niche occupancy and the relative role of microhabitat and diet in resource partitioning among pond dwelling tadpole. *South American Journal of Herpetology*, 4: 275-285. <http://dx.doi.org/10.2994/057.004.0311> .
- PELTZER, P.M. & LAJMANOVICH, R.C. 2004. Anuran tadpole assemblages in riparian areas of the middle Paraná River, Argentina. *Biodiversity and Conservation*, 13: 1833-1842. <http://dx.doi.org/10.1023/B:BIOC.0000035870.36495.fc> .
- POMBAL JR., J.P. 1997. Distribuição especial e temporal de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil. *Brazilian Journal of Biology*, 52: 217-229.
- POMBAL JR., J.P. & HADDAD, C.F.B. 2005. Estratégias e modos reprodutivos de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil. *Papeis Avulsos de Zoologia*, 45: 201-213.
- PROVETES, D.B.; GAREY, M.V.; DA SILVA, F.R. & JORDANI, M.X. 2012. Knowledge gaps and bibliographical revision about descriptions of free-swimming anuran larvae from Brazil. *North-Western Journal of Zoology*, 8: 283-286.
- RICHARDS, S.J. 2002. Influence of flow regime on habitat selection by tadpoles in an Australian rainforest stream. *Journal of Zoology (London)*, 257: 237-279. <http://dx.doi.org/10.1017/S0952836902000869> .
- RICO, M.; ROCHA, C.F.D.; BORGES-JÚNIOR, V.N.T. & VAN SLUYS, M. 2004. Breeding ecology of *Scinax trapicheiroi* (Anura, Hylidae) at a creek in the Atlantic Rainforest of Ilha Grande, southeastern Brazil. *Amphibia-Reptilia*, 25: 277-286. <http://dx.doi.org/10.1163/1568538041975143> .
- RODRIGUES, D.J.; LIMA, A.P.; MAGNUSSON, W.E. & COSTA, F.R.C. 2010. Temporary pond availability and tadpole species composition in Central Amazon. *Herpetologica*, 66: 124-

130. <http://dx.doi.org/10.1655/09-020R2.1>

ROSSA-FERES, D.C. & JIM, J. 1994. Distribuição sazonal em comunidades de anfíbios anuros na região de Botucatu, São Paulo. *Brazilian Journal of Biology*, 54: 323-334.

SALTHER, S.N. & DUELLMAN, W.E. 1973. Quantitative constraints associated with reproductive mode in anurans. Pp 229-249. In: J.L. Vial (ed.). *Evolutionary biology of the anurans. Contemporary research on major problems*. University of Missouri Press, Columbia. 498p.

SANTOS, T.G.; ROSSA-FERES, D.C. & CASATTI, L. 2007. Diversidade e distribuição espaço-temporal de anuros em região com pronunciada estação seca no sudeste do Brasil. *Iheringia*, 97: 37-49. <http://dx.doi.org/10.1590/S0073-47212007000100007>.

SÃO PEDRO, V.A.; DRUMMOND, L.O.; COSTA, H.C.; FERNANDES, V.D. & FEIO, R. 2008. Predação de embriões por girinos de *Bokermannohyla alvarengai* (Anura: Hylidae) e, riacho temporário na Serra do Ouro Branco, Minas Gerais, Brasil. *Boletim do Museu de Biologia Melo Leitão*, 24: 111-118.

SBH. 2012. Brazilian amphibians – list of species, <http://www.sberpetologia.org.br>. (Accessed on 9 October 2012).

SCHIESARI, L.; GORDO, M. & HÖDL, W. 2003. Treeholes as calling, breeding, and developmental sites for the Amazonian Canopy Frog, *Phrynohyas resinifictrix* (Hylidae). *Copeia*, 2: 263-272. <http://dx.doi.org/10.1643/0045-8511>.

SCHMIDT, B.R. & AMÉZQUITA, A. 2001. Predator induced behavioral responses: tadpoles of the neotropical frog *Phyllomedusa tarsius* do not respond to all predators. *Herpetological Journal*, 11: 9-15.

SILVA, F.R.; CANDEIRA, C.P. & ROSSA-FERES, D.C. 2012. Dependence of anuran diversity on environmental descriptors in farmland ponds. *Biodiversity and Conservation*, 21: 1411-1424. <http://dx.doi.org/10.1007/s10531-012-0252>.

SILVA, M. B. & JUNCÁ, F. A. 2006. Oophagy in tadpoles of *Leptodactylus troglodytes* (Amphibia, Anura, Leptodactylidae). *Sitientibus Série Ciências Biológicas*, 6: 89-91.

SMITH, M.J.; SCHREIBER, E.S.G.; SCROGGIE, M.P.; KOHOUT, M.; OUGH, K.; POTTS, J.; LENNIE, R.; TURNBULL, D.; JIN, C. & CLANCY, T. 2007. Associations between anuran tadpoles and salinity in a landscape mosaic of wetlands impacted by secondary salinisation. *Freshwater Biology*, 52: 75-84. <http://dx.doi.org/10.1111/j.1365-2427.2006.01672>.

SOUZA FILHO, I.F.; BRANCO, C.C.; CARVALHO-E-SILVA, A.M.P.T.; SILVA, G.R. & SABAGH, L.T. 2007. The diet of *Scinax angrensis* (Lutz) tadpoles in an area of Atlantic Forest (Mangaratiba, Rio de Janeiro) (Amphibia, Anura, Hylidae). *Revista Brasileira de Zoologia*, 24: 965-970. <http://dx.doi.org/10.1590/S0101-81752007000400012>.

STRAUß, A.; REEVE, E.; RANDRIANIAINA, R.D.; VENCES, M. & GLOS, J. 2010. The world's richest tadpoles communities show functional redundancy and low functional diversity: ecological

data on Madagascar's stream-dwelling amphibian larvae. *BMC Ecology*, 10: 1-10. <http://dx.doi.org/10.1186/1472-6785-10-12>.

TOFT, C.A. 1985. Resource partitioning in amphibians and reptiles. *Copeia*, 1985: 1-21.

TORRES-OROZCO, R.E.; JIMENEZ-SIERRA, C.L.; VOGT, R.C. & BENITEZ, J.L.V. 2002. Neotropical tadpoles: spatial and temporal distribution and habitat use in a seasonal lake in Veracruz, México. *Phyllomedusa*, 1: 81-91.

VAN SLUYS, M.; RICO, M. & ROCHA, C.F.D. 2006. Seasonal and hourly patterns of reproductive activity in *Scinax trapicheiroi*, (Anura, Hylidae), Rio de Janeiro State, southeastern Brazil. *Herpetological Journal*, 16: 15-20.

VASCONCELOS, T.S. & ROSSA-FERES, D.C. 2005. Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do Estado de São Paulo, Brasil. *Biota Neotropica*, 5: 1-14. <http://dx.doi.org/10.1590/S1676-06032005000300010>.

VASCONCELOS, T.S.; SANTOS, T.G.; ROSSA-FERES, D.C. & HADDAD, C.F.B. 2009. Influence of the environmental heterogeneity of breeding ponds on anuran assemblages from southeastern Brazil. *Canadian Journal of Zoology*, 87: 699-707. <http://dx.doi.org/10.1139/Z0-058>.

VASCONCELOS, T.S.; SANTOS, T.G.; ROSSA-FERES, D.C. & HADDAD, C.F.B. 2011. Spatial and temporal distribution of tadpole assemblages (Amphibia, Anura) in a seasonal dry tropical forest of southeastern Brazil. *Hydrobiologia*, 673: 93-104. <http://dx.doi.org/10.1007/s10750-011-0762-9>.

VRCIBRADIC, D.; TEIXEIRA, R.L. & BORGES-JÚNIOR, V.N.T. 2009. Sexual dimorphism, reproduction, and diet of the casque-headed treefrog *Itapotihyla langsdorffii* (Hylidae: Lophiohyliini). *Journal of Natural History*, 43: 2245-2256. <http://dx.doi.org/10.1080/00222930903015824>.

WEYGOLDT, P. & CARVALHO-E-SILVA, S.P. 1991. Observation on mating, oviposition, egg sac formation, and development in the egg-brooding frog, *Fritziana goeldii*. *Amphibia-Reptilia*, 12: 67-80.

WILD, E.R. 1996. Natural history and resource use of four Amazonian tadpole assemblages. *Occasional Papers of the Natural History Museum of the University of Kansas*, 176: 1-59.

ZIMMERMAN, B.L. & BIERREGAARD, R.O.Jr. 1986. Relevance of the equilibrium theory of island biogeography with an example from Amazonia. *Journal of Biogeography*, 13: 133-143.

ZIMMERMAN, B.L. & SIMBERLOFF, D. 1996. An historical interpretation of habitat use by frogs in Central Amazonian forest. *Journal of Biogeography*, 23: 27-46. <http://dx.doi.org/10.1046/j.1365-2699.1996.d01-218>.

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