Trait-environment relationship in tadpole communities of the southern Atlantic Forest

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The diversity of functional traits can be evaluated by analyzing an individual's morphological, physiological, and behavioral attributes, revealing the effect of environmental filters on communities. However, the role of different spatial scales in environmental evaluation over ecological attributes is complex and poorly studied in tadpole communities. Here, we investigated the association between micro (local) and macro (landscape) variables and the morphological traits of tadpoles in the southern region of the Brazilian Atlantic Forest. We sampled 28 waterbodies (ponds and streams) and evaluated 2861 individuals of 22 anuran species. Our sampling reached a wide geographic area across three states in southern Brazil. We measured the physicochemical characteristics of the water, as well as microhabitat and landscape environmental descriptors. Eighteen morphological traits were evaluated in individuals for each tadpole species. We performed RLQ and fourth-corner analyses to determine the patterns of trait-environment relationships and the local and landscape variables that influence the morphological characteristics of tadpoles. We found that morphological traits are mainly associated with physicochemical and microhabitat attributes and are distinct between ponds and streams. In ponds, tadpole traits exhibited greater association with water depth, pH, and the presence of vegetation, whereas in streams they were driven by several water physicochemical components and microhabitat composition. Our results indicate that local components of habitat (water characteristics and microhabitat) have a greater influence over functional traits of tadpoles than landscape in both ponds and streams. Furthermore, we also found possible adjustments in the functional traits of tadpoles related to the physicochemical characteristics of the water and microhabitat.

Keywords: Anurans, Freshwater, Functional diversity, Habitat, Morphology

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BACKGROUND

Functional traits are the main determinants of the biology of organisms, including biochemical, physiological, morphological, developmental, and behavioral mechanisms (Violle et al. 2007; Petchey et al. 2009). Researchers argue that studies based on functional groups provide a more direct investigation of ecological responses to environmental changes, thus favoring the comprehension of the processes involved in biological diversity and ecosystem functioning (Hoeinghaus et al. 2007; Goswami et al. 2017). The functional attributes can be measured and compared among species or individuals, providing elements about their ecological role in the community (Goswami et al. 2017). Functional diversity has been applied to analyze the trait-environment relationship in several taxa (Carvalho and Tejerina-Garro 2015; Liu et al. 2016), including plants, birds, fishes and amphibians (Arruda et al. 2018; Lescano et al. 2018; Jordani et al. 2019). These studies revealed that environmental conditions can act on communities by selecting species that have similar traits and allowing them to survive (Cornwell et al. 2006; Sobral and Cianciaruso 2012). The environmental filters can act at different scales, such as micro-spatial (local habitat characteristics) and macro-spatial (landscape characteristics), determining the patterns of community assembly (Weiher et al. 2011; Violle et al. 2012).

In the last decades, ecologists have been trying to understand how the assembly of species is organized based on the description of species richness and abundance (Gotelli and Colwell 2001). The “functional traits approach” may work as a new tool to help understand how environmental conditions affect individuals (Menezes et al. 2020), as well as their roles in ecosystem functioning (Haddad et al. 2015). By adding a functional traits approach, studies will move forward in understanding community ecology and individual contribution to ecosystem networking. Researchers have been applying functional diversity to investigate the ultimate consequences of the environment on individuals (Tilman et al. 1997; Diaz and Cabido 2001; Petchey et al. 2004; Hooper et al. 2005). Concerning the evaluation of functional traits, anurans were revealed to be a good model for studies due to their relatively high sensitivity to environmental changes (Preuss et al. 2020). This sensitivity has already been documented in terms of species diversity, which is affected by human-driven habitat changes, such as land use, changes in nutrient availability, and climatic conditions (Hooper et al. 2005). As anurans occur and reproduce in a variety of freshwater habitats, including ponds, streams, bromeliads, and many other permanent or temporary waterbodies (Altig and McDiarmid 1999), they show a great variation in terms of ecological and morpho-functional characteristics (Duellman and Trueb 1994; Sherratt et al. 2017 2018). For species with aquatic larvae, the physicochemical characteristics of the water represent a limiting factor for their survival. During their metamorphosis, individuals are exposed to water proprieties which could affect their metabolism (Afonso and Eterovick 2007), morphology, and physiology (Sipaúba-Tavares et al. 2007; Thomaz and Cunha 2010; Mansano et al. 2012 2014; Farquharson et al. 2016) and, consequently their general performance. In addition, microhabitat configuration would favor predation and/or competition pressures shaping the organization of tadpole communities (Wellborn et al. 1996; Werner et al. 2007; Melo et al. 2018).

In fact, many studies showed a direct relationship between aquatic microhabitat characteristics and the composition of tadpole communities. Some of them focused on nutrient availability (Williams et al. 2008; Queiroz et al. 2015), waterbody proprieties (Schiesari 2006; Williams et al. 2008; Thomaz and Cunha 2010 Queiroz et al. 2015), and water characteristics (Lima et al. 2003; Maciel and Juncá 2009; Mansano et al. 2018). However, the potential for the functional morphology of tadpoles to be influenced by landscape configuration is poorly explored (Queiroz et al. 2015; Marques et al. 2018; Santos et al. 2021). Although some recent studies turned their attention to the functional diversity of tadpoles, most of them focused on a local spatial analysis (Jordani et al. 2019; Dalmolin et al. 2020; Lipinski et al. 2020; Santos et al. 2021). Based on this, we aimed to study how the environment affects the functional traits of tadpoles in ponds and streams in both local and landscape scales.

MATERIALS AND METHODS

Study site

We carried out the study in waterbodies in Atlantic Forest habitats in southern Brazil, between coordinates 22º30' to 33º45'S (latitude) and 48º02' to 57º40'W (longitude) (Fig. 1). The landscape of the region is formed by Atlantic Forest and high-altitude grasslands (Veloso and Góes-Filho 1982; SOS Mata Atlântica and INPE 2008) with a variety of surrounding matrices including urban and rural areas with the presence of pastures and agricultural plantations (Ribeiro et al. 2009; Pillar and Vélez 2010). The climate is humid subtropical (IAP 2004), with rainfall ranging from 1600 to 2200 mm per year (Alvares et al. 2013). The wavy relief is formed by plateaus, plains and escarpments (IAP 2004), with areas of steep slopes and embedded valleys (Santa Catarina 1986). The altitude varies from 300 to 1200 m above sea level.

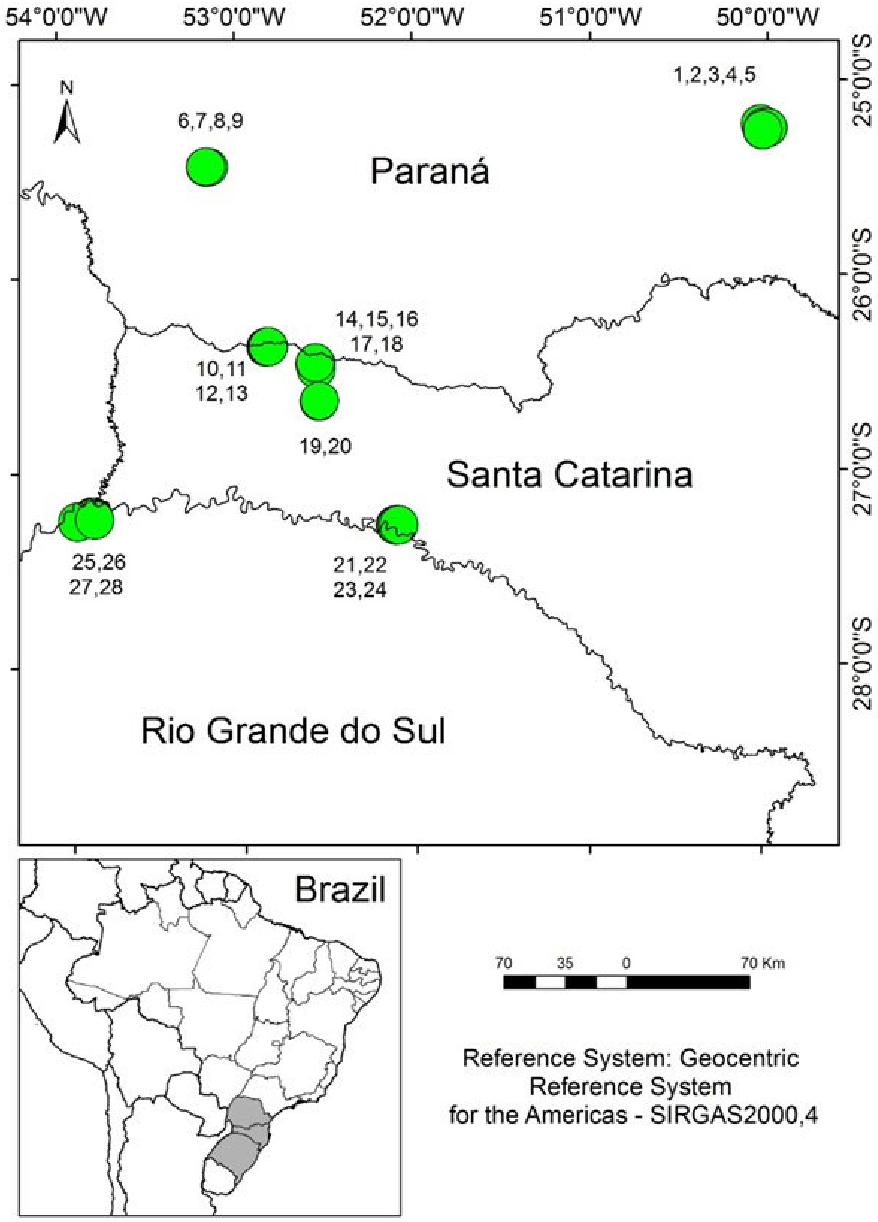

Fig. 1. Sampled waterbodies in areas of Atlantic Forest in southern Brazil. Numbers (from 1 to 28) refer to each waterbody sampled. For additional details, see Supplementary information (Fig. S1).

The selection of the sampling sites was based on the climatic, altitudinal and rainfall patterns and with a similar history of human interference. For this, we applied the following criteria for choosing sample areas: a) presence of well-preserved remnants of the Atlantic Forest (preferentially inside protected areas); b) similar climatic conditions of temperature and rainfall (Cfa and Cfb climatic pattern; Alvares et al. 2013); c) elevation up to 900 m above the sea level; d) similar topography and e) presence of ponds and streams used as breeding sites by anurans. Finally, the exact sampling point (waterbody), was defined based on prior knowledge of the occurrence of amphibians and of abiotic and biotic characteristics that indicate reproductive sites of anurans (shallow water, presence of floating vegetation, and abundant vegetation at the margins; Maltchik et al. 2011; Knauth et al. 2018).

Tadpole sampling

We sampled tadpoles in 28 waterbodies (13 ponds and 15 streams), from October 2018 to March 2019. The waterbodies consisted of permanent and semi-permanent ponds and streams that were associated with forest habitats. The mean distance between the waterbodies was 2.3 km ranging from 0.7 km to 280 km from each one. Distance between ponds was limited by the reduced availability of high-quality habitats encompassing ponds with a similar configuration of size, shape, and surrounding vegetation. Nevertheless, considering that our study was focused on the larval stage of anurans, whose displacement is limited to the interior of waterbodies, the spatial dependence between the samples was probably minimal even when adult anurans tend to move short distances daily (Oliveira et al. 2016). Due to logistic limitations and the required distance between sites, we adopted the strategy of sampling many and more distant sites once instead of sampling a few sites many times.

Samplings were performed from 0800AM to 0600PM, with the search standardized in one hour at each waterbody, within a single anuran breeding season. We performed a single sampling in each water body. This procedure was adopted considering a large sample area (see Fig. 1) and the reproductive period of amphibians in warm seasons in southern Brazil, which is favorable to detect most species (adults and tadpoles; Santos et al. 2020).

We captured tadpoles using a wired dip net with a mesh size of 3 mm and a diameter of 300 mm (Heyer 1976) and sweeping all available microenvironments at the margin of the waterbody, where tadpoles are more easily captured (Vasconcelos and Rossa-Feres 2005; Santos et al. 2007; Both et al. 2009; Bolzan et al. 2016). We searched through the whole margin of the ponds and, for the streams, all possible locations were searched, covering a stretch of approximately 100 m of linear margin (adapted from Jordani et al. 2017). We defined 100 m intending to achieve a sampling effort similar to that applied to ponds. This definition was based on previous tests, from which we conclude that sampling along a 100-m stretch of a stream involved an amount of time similar to sampling a single pond, and a similar number of tadpoles was captured. As the aquatic vegetation seems to affect the presence of tadpoles (Maltchik et al. 2011; Knauth et al. 2018), we define the exact position of each transect across the stream to include the highest possible variation in marginal vegetation (density and variety of grass, shrubs, and trees). Immediately after capture, the tadpoles were euthanized, following the Brazilian regulations for the use of animals (CONCEA 2018), by immersion in a 2% lidocaine solution. Afterward, they were individualized and stored in containers with absolute ethanol. To avoid any effect of the preservation method over morphology, all measurements were performed few days after the sampling. We used absolute ethanol for preservation to adjust our protocol to a set of parallel studies that our sampling is part of, specifically about fungus (Bd) monitoring program. In the laboratory, we identified each specimen with the aid of a stereomicroscope and identification keys (*e.g.*, Machado and Maltchik 2007; Gonçalves 2014).

Environment descriptors of waterbodies

We considered 33 environmental variables for each waterbody (Table 1). Variables were classified as (1) local environmental descriptors (physicochemical characteristics of the water and microhabitat configuration) and (2) landscape environmental descriptors. Regarding local descriptors, we measured 12 physicochemical characteristics of the water and 16 microhabitat components. Regarding the landscape, we evaluated five variables. All evaluated variables are listed in table 1, followed by a brief explanation of their relevance in an ecological context.

Table 1. Environmental variables measured from sampled ponds and streams in tadpole collections. (A) Physicochemical – local scale, (B) Microhabitat – local scale and (C) Landscape-scale

Local Scale part A – Water physicochemical analysis		
Definition of the environmental variable (Code)	Variable	Ecological relevance
Total alkalinity (total_alk)	Continuous	Indicates the concentration of carbonate and bicarbonate salts. It is associated with the formation of the plankton shell (1).
Bicarbonate (Alk_HCO3)	Continuous	Acts on pH balance (1).
Total Phosphorus (P)	Continuous	Is related to respiration and photosynthetic metabolism (phytoplankton production) (1).
Chemical Oxygen Demand (COD)	Continuous	Availability of organic matter (2).
Ammonia (NH3) Nitrate (NO3-) Nitrite (NO2-)	Continuous Continuous Continuous	The three are related to the excretion of aquatic organisms and the decomposition of organic matter by nitrifying bacteria (1).
pH (water_pH) = recorded in the field with multi-parameter measurer.	Continuous	Indicates the concentration of hydrogen ions (H +) and its variation is associated with the CO_2 released during phytoplankton photosynthesis (1).
Temperature (water_temp) = Water temperature in ºC, recorded in the field with multi-parameter measurer.	Continuous	Influences the metabolism of tadpoles by accelerating or inhibiting their growth (3, 4).
Dissolved oxygen (diss_oxi) = Dissolved oxygen, recorded in the field, in mg L^{-1}, with multi-parameter measurer.	Continuous	Related to tadpole breathing and decomposition of organic matter by bacteria (2).
Electrical Conductivity of water (water_conduct) = Electrical conductivity, recorded in (μScm^{-1}), with multi-parameter measurer.	Continuous	Related to the decomposition of organic matter (high) and primary production (phytoplankton; low). Food availability in water (5, 6, 7).
Transparency (water_transp) = Water transparency measured in centimeters with a Secchi disk and visual inspection to shallow.	Continuous	Related to the concentration of organic matter, sediments and phytoplankton, food resources (2).
Local Scale part B - Microhabitat		
Pond depth/stream depth (depth) = Water depth measured in centimeters, from the pond margin and the center of the stream. Pond_area/Stream_area = Area of pond/area of stream in meters, measured from the measuring tape and complemented with Google Earth.	Continuous Continuous	Both are related to the occurrence and persistence of species in ponds, to competition/predation, and, consequently to reproductive success (8, 9, 10).
Canopy opening (canopy-open) = Canopy opening recorded in percentage.	Continuous	Influences the performance of tadpoles and changes the structure of the community (11, 12).

Aquatic vegetation (aqua_veg) = Presence/absence of submerged aquatic vegetation in the pond or stream.	Categoric	Provides a greater variety of microhabitats, increasing biodiversity and the availability of resources (13).
Grasses (grass) = Presence/absence of helophyte plants in the pond or stream.	Categoric	Substrate types are related to habitat selection, species segregation, niche partition between species and availability of resources (10, 14, 15).
Rocks (rocks) = Presence/absence of rocks only at the bottom of a pond or stream.	Categoric	
Grasses and rocks (grass_rocks) = Presence/absence of rocks and herbaceous plants in the pond or stream.	Categoric	
Leaves, roots and rocks (leave_roots_rocks) = Presence/absence of leaves, roots and rocks in the pond or stream.	Categoric	
Mud (mud) = Presence/absence of mud at the bottom of a pond or stream.	Categoric	
Mud and rocks (mud_rocks) = Presence/absence of rocks and grass at the bottom of a pond or stream.	Categoric	
Roots and rocks (roots_rocks) = Presence/absence of roots and rocks at the bottom of a pond or stream.	Categoric	
Grasses monoculture (grass_mon) = Presence/absence of grassland type of terrestrial vegetation occupying the pond/stream margin.	Categoric	Influences the flow of organic matter, primary production (phytoplankton) and changes the structure of the community. Provides habitat, breeding sites and foraging areas (12).
Grasses and trees (grass_trees) = Presence/absence of grass and tree type of terrestrial vegetation occupying the pond/stream margin.	Categoric	
Shrubs (shrubs) = Presence/absence of shrub type of terrestrial vegetation occupying the pond/stream margin.	Categoric	
Trees (trees) = Presence/absence of tree type of terrestrial vegetation occupying the pond/stream margin.	Categoric	
Edge distance (edge distance) = Distance from the waterbody to the forest edge.	Continuous	
Landscapes-scale		
Agriculture area (Agriculture) = areas with corn, soy, wheat and pasture cultivation	Continuous	Favors the occurrence and occupation in ponds (16), influences predation, shelter and risk of desiccation (17).
Aquatic environment area (Aqua_envir) = watercourses, lakes and ponds.	Continuous	
Forest area (Forest) = areas of native forest in secondary and advanced successional stage.	Continuous	
Pasture area (Pasture) = areas with natural pastures, native grassy environments or livestock.	Continuous	
Urbanization area (Urbanization) = secondary access roads, residential or commercial buildings.	Continuous	

References: (1) Mansano et al., 2018; (2) Borges et al., 2014; (3) Lima et al., 2003; (4) Maciel and Juncá 2009; (5) Sipaúba-Tavares et al., 2007; (6) Mansano et al., 2012; (7) Mansano et al., 2014; (8) Wellborn et al., 1996; (9) Werner et al., 2007; (10) Melo et al., 2018; (11) Schiesari, 2006; (12) Williams et al., 2008; (13) Thomaz and Cunha 2010; (14) Pianka 1973; (15) Eterovick and Barata 2006; (16) Mazerolle et al., 2005; (17) Pulsford et al., 2019.

Local descriptors

Local descriptors are based on water and microhabitat evaluation. Water samples were randomly collected at each tadpole collection site, 10 cm from the waterbody's edge. We collected samples of surface water (15 cm deep) using sterilized dark plastic bottles (500 ml) that were immediately placed in a refrigerated box until the physicochemical analysis. Analysis was performed at least three days after samples were collected. We evaluated the total alkalinity (Total_alk), bicarbonate (Alk_HCO3), total phosphorus (P), chemical oxygen demand (COD) and nitrogen in ammonia (NH3), nitrite (NO2-) and nitrate (NO3-) (APHA 1998; Ternus et al., 2011). In the field, we collected data on pH (water_pH), temperature (water_temp) (ºC), dissolved oxygen (dissol_oxi) in mgL^{-1} and electrical conductivity (water_conduct) (μScm^{-1}) using a multiparameter meter (*Lovibond Sensodirect* 150. manufactured in the USA). Water transparency was measured with the Secchi disk by inserting it approximately 15 cm deep. For shallower water bodies where it was not possible to apply the standard Secchi disk protocol, we visually estimated the transparency, recording its maximum viewing depth. The transparency was measured at the same tadpole-collection points and was done on the banks of the ponds and at the midpoint of the streams. All data were taken by the same observer to avoid skewed weightings. These variables are considered important for tadpoles since water quality has a direct influence on their behavior and development and an indirect influence on food availability (Castaneda 2014; Zongo and Boussim 2015).

Regarding the microhabitat evaluation in each waterbody, we measured the water depth, waterbody area, and canopy opening and performed and described the vegetation and the substrate inside and outside waterbodies. The area of ponds and streams was recorded at the site using a measuring tape (in meters). For ponds, the measurement of the area was complemented with images of polygon area (*Google Earth images*), and, for streams, the area was determined by the individual width x length considering the distance of up to 100 m in each stream. Water depth was measured at three points for each waterbody at the same location where tadpoles were sampled. The canopy opening was measured using a spherical lens (*Universal clip lens*; 180º) coupled to a cell phone (*Xiaomi MI*) at the tadpole-collection point and later treated in the *GapLight* program version 2.0 (Frazer et al. 1999) and presented as a percentage. For the canopy opening, we conducted a single measurement per water body at the edge of the pond and in the center of the stream.

Substrate cover was evaluated by a systematic visual inspection. For the qualitative recording of the substrate and terrestrial vegetation, we used four quadrats of 4 m² in the interior and banks of the water bodies, with the margins of the ponds and the 100 m transects in the streams as the recording point. Finally, the distance from the forest edge was measured in meters using tape from the edge of the pond/stream to the transition point of forest vegetation with roads and/or open areas. We identified eight predominant categories of substrate cover: aquatic vegetation (aquatic_veg), grasses (grass), rocks (rocks), grasses and rocks (grass_rocks), leaves, roots and rocks (leave_roots_rocks), mud (mud), mud and rocks (mud_rocks) and roots and rocks (roots_rocks). As aquatic vegetation (aqua_veg), we consider the presence of hydrophytes and macrophytes that are completely submerged (*e.g.*, *Elodea* sp.) and, as grasses, we consider helophytic plants that are partially submerged (*e.g.*, Cyperaceae). Following, we recorded and classified the waterbody's terrestrial or marginal vegetation into four types: grasses (grass), grasses and trees (grass_trees), shrubs (shrubs), and trees (trees). We considered phorophytes > 2 m as trees and < 2 m as shrubs, while grasses included native herbaceous plants (*e.g.*, Cyperaceae, Poaceae and Typhaceae) and pasture monocultures (*e.g.*, *Brachiaria* sp.).

Landscape descriptors

We assessed land use based on the analysis of satellite images (Landsat 8 multispectral images, sensor Operational Land Imager from the U.S. Geological Survey; https://earthexplorer.usgs.gov). We used images captured in the year of sampling (2019) that had minimal cloud cover without significant radiometric noise. We performed the following pre-processing steps of the images: 1) geometric corrections, due to the inherent geometric distortions that images collected at different times through the georeferencing of these images; 2) atmospheric corrections to reduce the interference of atmospheric scattering on the images (Soares et al. 2015); and 3) mosaic and enhancement of the different images in each season to reduce the seasonal effects on the visual aspect of the images. Pre-processing was done using the *ENVI* software, version 5.51 (L3Harris Geospatial, Boulder, Colorado, USA). After the pre-processing steps, we defined classes of land use and occupation based on on-site observations, considering the predominant use of the areas. The categories were established as Agriculture area, Aquatic environments area, Forest area, Pastures area, and Urbanization area (Table 1). We classified the images based on their vectorization in ArcGIS software version 10.3 (Esri, Redlands, California, USA), considering the buffer with a 250-m radius for each waterbody. The buffer size was based on previous studies that describe the average habitat size for amphibians, ranging from 290 m (Semlitsch and Bodie 2003) to 500 m (Canessa and Parris 2013). We consider the central point of the buffer to be the pond or stream (collection points). The polygons for each type of roof were redesigned for the SIRGAS 2000 reference system, Universal Transverse Mercator (UTM) projection, zone 22S, and we calculated the areas in km².

Functional traits of tadpoles

For the analysis of functional traits diversity, we recorded measurements from one to ten tadpoles of each species. Eighteen morphological traits were evaluated for each species in the study area. The measured functional traits consider the functional characteristics related to the main aspects of the resource acquisition, use of resources and life-history strategies, as follows: tail muscle height (TMH), tail muscle width (TMW), dorsal fin height (DFH), ventral fin height (VFH), body height (BH), body width (BW), body length (BL), oral disk size (ODS), oral disc position (ODP), number of tooth rows (NTR), eye size (ES), internal eye distance (IED), eye position (EP), nostril size (NS), internal nostril distance (IND), nostril position (NP), spiracle length (SL), spiracle width (SW), spiracle position (SP). We also recorded the position in the water column (benthic, nektonic and neustonic), the presence of flagellum (present/absent), and the ontogenetic development stage (Fig. 2; Table 2). The classification of the tadpole position in the water column was defined according to the literature (see Queiroz et al. 2015).

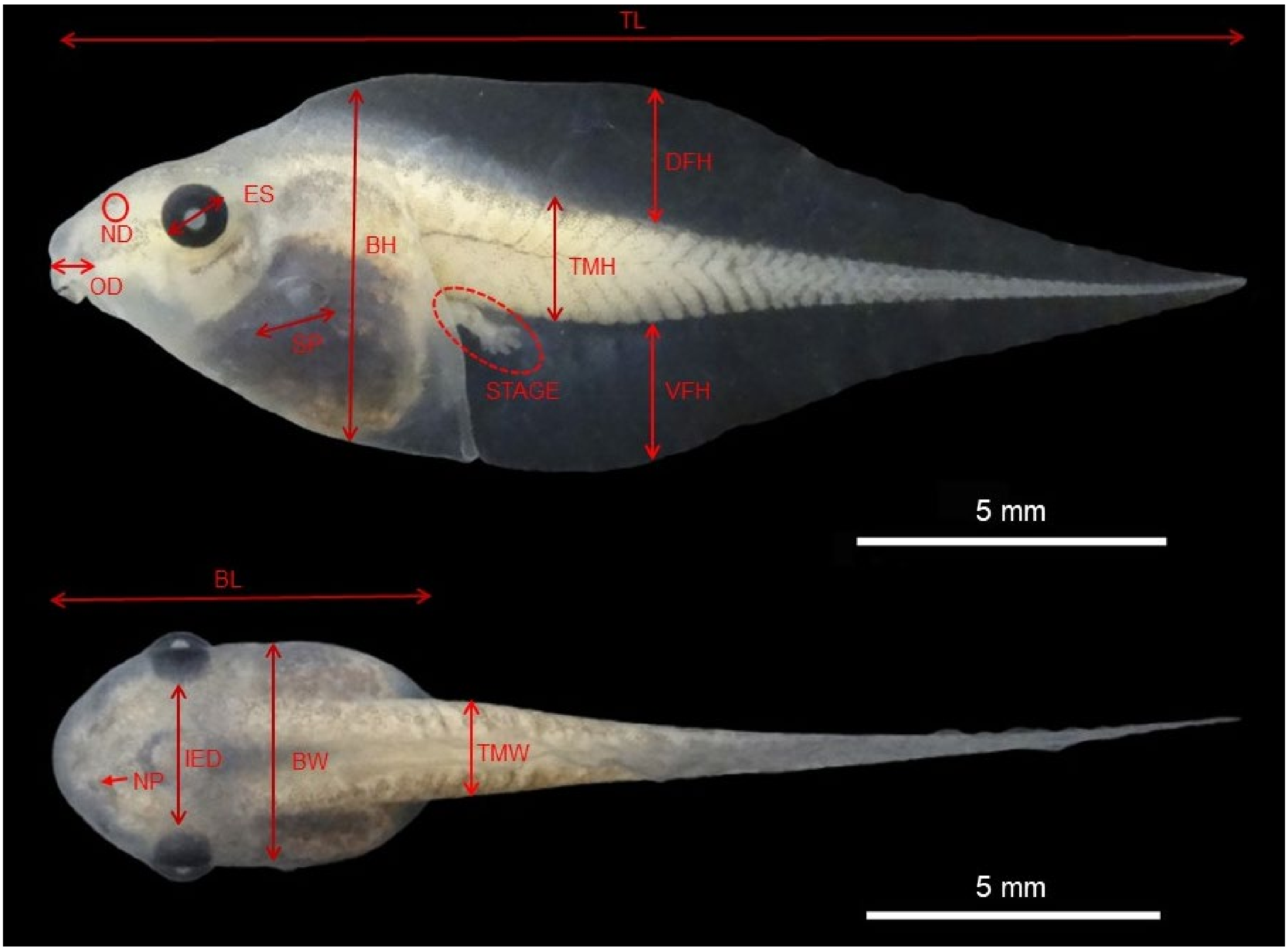

Fig. 2. Morphological metrics evaluated in anuran tadpoles: total length (TL); body length (BL); tail muscle height (TMH); tail muscle width (TMW), dorsal fin height (DFH), ventral fin height (VFH), body height (BH), body width (BW), oral disk size (ODS), oral disc position (ODP), number of tooth rows (NTR), eye size (ES), internal eye distance (IED), eye position (EP), nostril size (NS), internal nostril distance (IND), nostril position (NP), spiracle length (SL), spiracle width (SW), spiracle position (SP). In this picture: Dorsal view and lateral view of *Scinax fuscovarius* tadpoles. (Photographed by Brena da Silva Gonçalves).

Table 2. Functional traits measured from different functional characteristics of tadpoles present in the sampled waterbodies

Functional trait	Variable	Ecological relevance
Body Height (BH) = body height/total length	Continuous	Associated with tadpole biomass; also determines the position of the species in the water column (1, 2, 3, 4)
Body Length (BL) = Body length/total length	Continuous	
Body Width (BW) = Body width/total length	Continuous	
Tail Muscles Width (TMW) = maximum width of the caudal musculature/body length	Continuous	Related to the species' swimming capacity, the exploration of micro-

Dorsal Fin Height (DFH) = maximum height of dorsal fin/maximum height of the caudal musculature	Continuous	habitats and, in the case of nektonic tadpoles, the maintenance of balance when they are at rest (1, 2, 4, 5, 6)
Ventral Fin Height (VFH) = maximum height of ventral fin/maximum height of the caudal musculature	Continuous	
Internal Eye Distance (IED) = distance between eyes/body length	Continuous	Related to habitat exploration and the species' ability to detect predators (1, 2, 4)
Eye Size (ES) = eye diameter/body length	Continuous	
Number of Tooth Rows (NTR) = Sum of number of front and back rows	Continuous	Directly related to the ability to exploit food resources (1, 2)
Oral Disc Position (ODP) = Anteroventral; ventral	Categoric	
Mouth Size (MS) = mouth size/body length	Continuous	
Presence of flagellum = Present or absent	Binary	Assists in capacity and speed during swimming (5, 6)
Nostrils Diameter (ND) = nostril diameter/body length	Continuous	Directly related to the circulation of water in the body, in addition to assisting the chemical perception of molecules dissolved in water (1, 4)
Nostrils Position (NP) = Absent/laterodorsal/ dorsolateral/ anterolateral/lateral/dorsal	Categoric	
Spiracle Length (SL) = Body length/total length	Continuous	The spiracle, together with the operculum, is associated with the regulation and control of respiratory and feeding currents (7, 8)
Spiracle Position (SP) = Ventral/sinistral/posterodorsal/posterior	Categoric	
Spiracle Width (SW) = Body Width/Total Length	Continuous	

REFERENCES: (1) Altig and Johnston 1989; (2) Altig and McDiarmid 1999; (3) Buskirk 2009; (4) Jordani et al., 2019; (5) Johnson et al., 2015; (6) Queiroz et al., 2015; (7) Gollmann and Gollmann 1999; (8) Altig 2006.

Data analysis

Before carrying out the statistical analyses, we transformed our quantitative datasets (functional traits and environmental descriptors) through a natural log transformation; this procedure allows obtaining a normal distribution of the different datasets. Subsequently, we used a combination of the RLQ (Dolédec et al. 1996; Dray et al. 2016) and the fourth-corner analysis (Legendre et al. 1997) for assessing the responses of the set of tadpole functional traits to environmental variation (Dolédec et al. 1996; Dray et al. 2014). In a general view, the proposed RLQ approach is an analysis that performs ordering analyses based on the combination of the following data matrices: an environmental matrix by sites (*R*; site x environment), a species-by-sites matrix (*L*; site x species), and a functional-trait by species matrix (*Q*; species x traits). Matrices R and Q are linked by matrix L. The RLQ method is a multivariate technique that performs a double inertia analysis of matrices R and Q, assuming that matrix L is the link between environment and species traits (Dray et al. 2014).

Before the extended RLQ analysis, we ran the extended version of the fourth-corner approach with 9999 permutations to test the correlations between functional traits and environmental descriptors. For this, we applied the null model 6 (which fixes the level of type I error; Dray et al. 2016). To prepare the matrices for the extended RLQ analysis, all matrices were analyzed separately with different ordinations: the species-by-site matrix (L) was analyzed using correspondence analysis (CA); the environmental matrix (R) was analyzed by principal component analysis (PCA); finally, the trait distance matrix (Q) was analyzed by principal coordinate analysis (PCoA). The fourth-corner method also combines matrices R, L and Q into a single matrix describing traits-environment associations (fourth-corner matrix; Legendre et al. 1997). Additionally, this analysis tests the relationship between one trait and one environmental variable at a time, allowing the evaluation of individual trait-environment relationships. RLQ and fourth-corner are complementary methods and their combined use may improve strongly the study of trait-environment associations (Dray et al. 2014). The RLQ analysis and the fourth-corner test were implemented using the packages “spdep” (Bivand et al. 2008) and “ade4” (Dray and Dufour 2007) of R software.

We ran the statistical procedures described above separately for each set of environmental data (i.e., one analysis for local environment data, and another for landscape data) and each type of aquatic system (i.e., ponds and streams). To avoid the inclusion of non-significant environmental descriptors in our models, we performed the analytical procedures described above in two steps. In the first step, we run the analyses containing the full model of environmental descriptors for each dataset (that is, local and landscape descriptors). Subsequently, we performed a new analysis and included only the environmental descriptors that showed significant relationships with the functional traits of the tadpoles (i.e., a selected model). The percentage of co-inertia is available as the link between functional traits and environmental descriptors.

RESULTS

Ponds and streams evaluation

We recorded a total of 22 species of eight families and 10 genera. Ponds and streams shared species been 14 of 22 registered in ponds and 19 in streams. Hylidae was the most representative family, with four genera (*Aplastodiscus*, *Boana*, *Dendropsophus* and *Scinax*). The genera *Elachistocleis*, *Proceratophrys* and *Lithobates* occurred only in ponds and the genus *Crossodactylus* only in streams (see Table S1). The species *Boana curupi* and *Crossodactylus schmidti* are considered forest specialists, while the others are considered habitat generalists (see Santos et al. 2021).

Patterns of trait-environment relationships in ponds

The percentage of co-inertia explained by the two first axes of the fitted RLQ was 75% for the model with local environmental descriptors and 80% for the model with landscape descriptors (Table 3). However, only the model with local environmental descriptors was significant (Std. observed = 3.69, p = 0.001; see Table S2).

Figure 3a–d presents the patterns of trait-environment relationships observed in ponds. The first RLQ axis had the strongest correlation with the local environmental descriptors pond depth and water pH, and with the functional traits related to the body: Spiracle position posterodorsal (SP posterodorsal), internal eyes distance, and eyes position dorsal (IED; EP dorsal), nostrils position dorsal (NP dorsal) dorsal tail height and flagellum absent (DFH; Fl absent). The second RLQ axis had the strongest correlation with trees, water conductivity, and the functional traits related to nostril position (NP absent) and dorsal tail height (DFH; see Tables S8–S10). Benthic tadpoles were more associated with high values of water pH, while nektonic tadpoles were more associated with the presence of trees, although no significant relation of this local environmental descriptor was detected for any of the measured functional traits. Finally, deeper water was more associated with the neustonic tadpoles (Fig. 3 a–b). The significance tests of trait-environment relationships are presented in figure 4a and the tables S3 and S4.

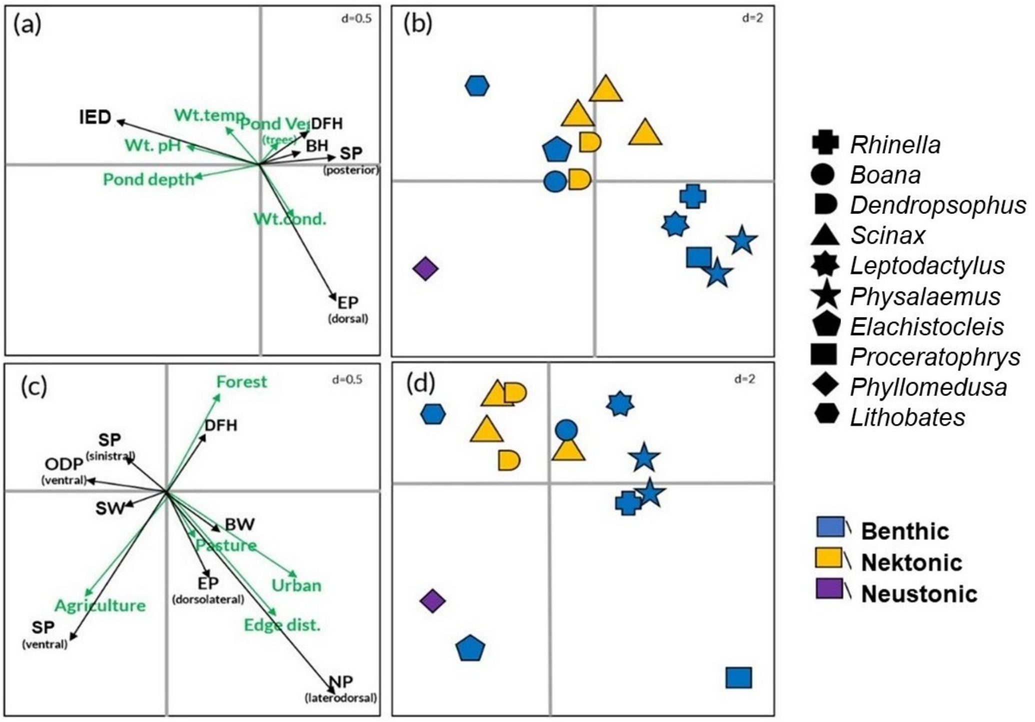

Fig. 3. Ordination of tadpoles' functional traits and ponds' local descriptors (a), anuran genera and tadpoles' ecomorphological guild (b), ordination of functional traits and landscapes descriptors (c) anuran genera and tadpoles' ecomorphological guild (d) result of the RLQ analysis. Genera (b and d) are presented by symbols and tadpole ecomophologic guilds by colors: blue = benthic; yellow = nektonic; purple = neustonic. In (a): IED = Internal eye distance; EP (dorsal) = Eye position dorsal; DFH = Dorsal fin height; BH = Body height; SP (posterior) = Spiracle position posterior; Wt.temp. = Water temperature; Wt.pH = Water pH; Wt.cond. = Water conductivity; Pond.veg.(grass) = Pond vegetation grass. In (c): BW = Body width; EP (dorsolateral) = Eye position dorsolateral; SP (ventral) = Spiracle position ventral; SP (sinistral) = Spiracle position sinistral; NP (laterodorsal) = Nostril position laterodorsal; ODP (ventral) = Oral disc position (ventral); SW = Spiracle width; DFH = Dorsal fin height; Edge dist. = Edge distance.

Table 3. RLQ results from ponds, model of local descriptors, and landscape descriptors at 28 waterbodies in areas of Atlantic Forest in southern Brazil

Model	Axis	Global RLQ			Fitted RLQ		
		Eigenvalue	%	Cum.%	Eigenvalue	%	Cum.%
Local Descriptors	1	4.44	49.10	49.10	4.10	57.84	57.84
	2	1.91	16.21	65.31	1.22	17.25	75.09
	3	0.96	8.55	73.86	0.79	11.07	86.16
	4	0.82	4.13	77.99	0.47	6.69	92.84
	5	0.50	2.06	80.05	0.36	5.04	97.89
Landscape Descriptors	1	2.13	40.70	40.70	1.98	55.09	55.09
	2	1.69	32.21	72.91	0.92	25.68	80.76
	3	0.75	14.37	87.28	0.68	18.89	99.65
	4	0.54	10.34	97.62	0.01	0.21	99.87
	5	0.12	2.19	99.80	<0.01	0.13	100.00

The first two axes of the RLQ model for the landscape descriptors of ponds accounted for, respectively, 55% and 26% of the variance. Despite this, this model was not statistically significant (Std. observed = 1.447, p = 0.07; Table 3, Fig. 3 c–d). However, the fourth-corner test showed significant relationships between some landscape descriptors and functional traits (Fig. 4b). We observed a negative relationship between forest and dorsal fin height (DFH); agriculture and spiracle position ventral (SP ventral); pasture and spiracle width (SW); urban and oral disc position ventral (ODP ventral), spiracle position sinistral (SP sinistral), and nostril position laterodorsal (NP laterodorsal); edge distance and body width (BW), oral disc position ventral (ODP ventral), spiracle position sinistral (SP sinistral) and nostril position (NP laterodorsal). Finally, we observed positive relationships between forest and spiracle position ventral (SP ventral), and urban and eye position lateral (EP lateral) (Tables S5 and S6).

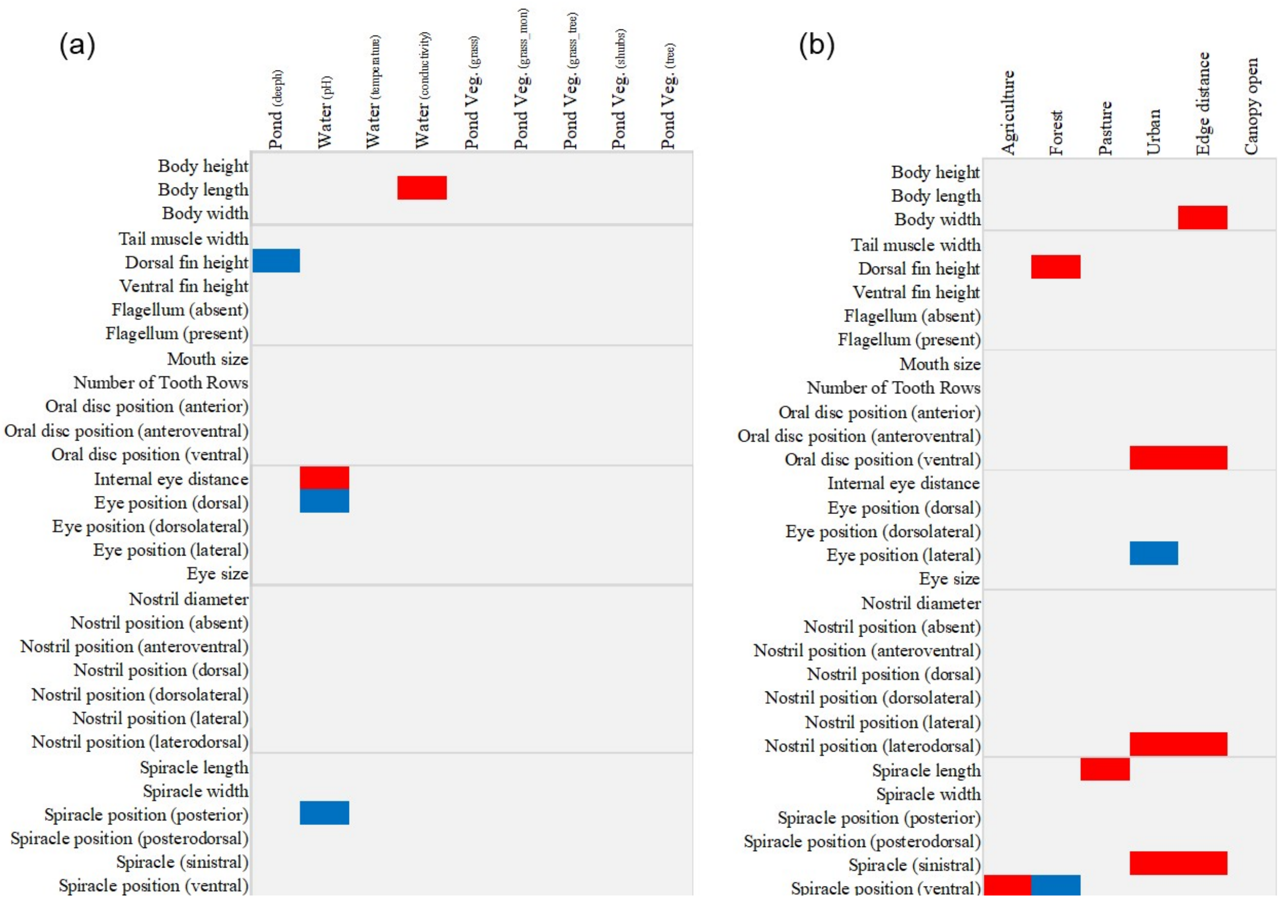

Fig. 4. Schemes representing the associations between the tadpoles' functional traits and ponds' local descriptors (a) and the associations between the tadpoles' functional traits and ponds' landscape descriptors (b). Colorless cells represent non-significant associations. Positive and negative associations are represented in blue and red, respectively. The lines show the attribute categories of the body, tail, mouth, eyes, nostrils, and spiracle. For functional traits, see Table 2. Acronyms of environment attributes in (a): Pond (depth) = pond water depth; Wt (pH) = Water pH; Wt (temp)

= Water temperature; Wt (cond) = Water conductivity; Pond veg. (grass) = Pond vegetation grasses; Pond veg. (grass_mon) = Pond vegetation grass monoculture; Pond veg. (grass_trees) = Pond vegetation grasses and trees; Pond veg. (shrubs) = Pond vegetation shrubs; Pond veg. (trees) = Pond vegetation trees.

Patterns of trait-environment relationships in streams

The percentage of co-inertia explained by the two first axes of the fitted RLQ was 73% for the model with local descriptors, and 78% for the model with landscape descriptors (Table 4). Similar to the patterns observed in ponds, only the model with local descriptors was significant (Std. observed = 3.54, p = 0.001; see Table S7).

Table 4. RLQ results from streams, model of local descriptors, and landscapes descriptors at 28 waterbodies in areas of Atlantic Forest in southern Brazil

Model	Axis	Global RLQ			Fitted RLQ		
		Eigenvalue	%	Cum.%	Eigenvalue	%	Cum.%
Local Descriptors	1	9.50	46.15	46.15	8.40	48.46	48.46
	2	5.56	27.04	73.19	4.25	24.50	72.96
	3	2.31	11.20	84.39	2.03	11.73	84.69
	4	1.23	5.99	90.39	0.97	5.58	90.27
	5	0.98	4.78	95.17	0.85	4.92	95.19
Landscapes Descriptors	1	4.72	48.43	48.43	2.51	56.84	56.84
	2	2.27	23.30	71.73	0.96	21.67	78.51
	3	1.11	11.43	83.16	0.46	10.37	88.88
	4	0.67	6.93	90.09	0.35	7.81	96.69
	5	0.47	4.79	94.89	0.12	2.71	99.40

Figure 5a-d presents the patterns of trait-environment relationships observed in streams. The first RLQ axis had the strongest correlation with water pH, water temperature, water conductivity, total alkalinity, Alk HCO3, and substrate stream with mud and rocks (mud_rocks; Tables S5–S7), and with the functional traits related to the body: Body width (BW) and spiracle position posterodorsal (SP posterodorsal), eye position dorsal and lateral (EP dorsal; EP lateral), number of tooth rows and oral disc position anteroventral (NTR; ODP anteroventral), mouth size (MS) and tail with flagellum present (Fl present) and ventral fin height (VFH; Tables S8 and S9). The second RLQ axis had the strongest correlation with the types of stream vegetation with the presence of trees on the banks and presence of grass and rocks on the substrate and with the functional traits related to the mouth size (MS). Most benthic tadpoles were more associated with the physicochemical descriptors of water (pH, temperature) and with trees, while the second group of benthic species (consisting of the genera *Aplastodiscus*, *Boana,* and *Lithobathes*) was more associated with the physicochemical descriptors of water NO3, Alk HCO3, total alkalinity and conductivity. Nektonic tadpoles were more associated with stream area and water transparency. Finally, the neustonic tadpoles were more associated with the presence of aquatic vegetation on the stream substrate (Fig. 5a–b). The significance tests of trait-environment relationships are presented in figure 6a.

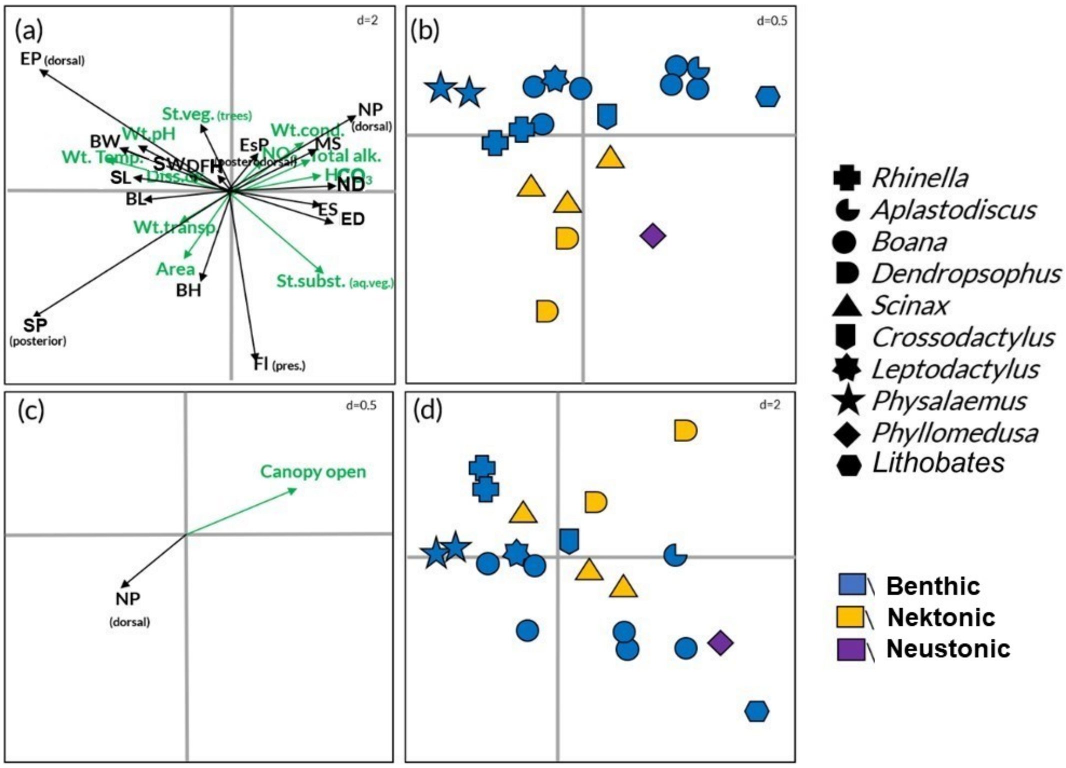

Fig. 5. Ordination of tadpoles' functional traits and stream' local descriptors (a), anuran genera and tadpoles' ecomorphological guild (b), ordination of functional traits and landscapes descriptors (c) anuran genera and tadpoles' ecomorphological guild (d) result of the RLQ analysis. Genera (b and d) are presented by symbols and tadpole ecomophologic guilds by colors: blue = benthic; yellow = nektonic; purple = neustonic. In (a): BH = Body height; BL = Body length; BW = Body width; DFH = Dorsal fin height; IED = Internal eye distance; ES = Eye size; EP (dorsal) = Eye position dorsal; Fl (pres.) Flagellum presence; ND = Nostril diameter; MS = Mouth size; SL = Spiracle length; SP (posterior) = Spiracle position posterior; SP (posterodorsal) = Spiracle position posterodorsal; SW = Spiracle width; Wt.temp. = Water temperature; Wt.pH = Water pH; Wt.cond. = Water conductivity; Pond veg. (Grass) = Pond vegetation grass. In (c): NP (dorsal) = Nostril position dorsal.

The two first axes of the RLQ model to the landscape descriptors of streams accounted for, respectively, 57% and 22% of the variance. Despite this, this model was not statistically significant (Std. observed = 1.33, $p = 0.09$; Table 4; Tables S10 and S11). However, the fourth-corner test showed significant relationships between canopy opening and the functional trait nostril position dorsal (NP dorsal) (Fig. 6b; Table S11).

Fig. 6. Schemes representing the associations between the tadpole functional traits and stream local descriptors (a) and the associations between the tadpole functional traits and stream landscapes descriptors (b). Colorless cells represent non-significant associations. Positive and negative associations are represented in blue and red, respectively. The lines show the attribute categories of the body, tail, mouth, eyes, nostrils and spiracle. For functional traits, see Table 2. Abbreviations of environment attributes, in (a): Stream (area) = Stream area; Wt (transparency) = Water transparency;

Wt (pH) = Water pH; Wt (temperature) = Water temperature; Wt (dissol_oxi) = Water dissolved oxygen; Wt (cond) = Water conductivity; Wt (COD) = Water chemical oxygen demand; Wt (NO2-) = Water nitrite; Wt (total_alk) = Water total alkalinity; Wt (Alk_HCO3) = Bicarbonate alkalinity; Str_Veg (trees) = Stream vegetation trees; Str_Veg (shrubs) = Stream vegetation shrubs; Str_Veg (grass) = Stream vegetation grasses; Str_Veg (grass_trees) = Stream vegetation grasses and trees; Str_subs (aqua_veg) = Stream substrate with aquatic vegetation; Str_subs (grass) = Stream substrate with grasses; Str_subs (rocks) = Stream substrate with rocks; Str_subs (grass_rocks) = Stream substrate with grasses and rocks; Str_subs (leave_roots_rocks) = Stream substrate with leaves, roots and rocks; Str_subs (mud) = Stream substrate with mud; Str_subs (mud_rocks) = Stream substrate with mud and rocks; Str_subs (roots_rocks) = Stream substrate with roots and rocks.

DISCUSSION

Our results pointed out that the local habitat variables are more relevant than the landscape to define functional traits in tadpole communities. Based on the differences between ponds and streams on their abiotic (Smith et al. 2002; Fairchild and Velinsky 2006; Hoeinghaus et al. 2007) and biotic components (Schriever and Lytle 2016; Jordani et al. 2017), we predicted that communities were exposed to different selective pressures that affect tadpole traits differently. This idea is supported by previous studies in which environmental characteristics, including properties of the waterbody, are important drivers for variations in tadpole morphology (Sun et al. 2021). Furthermore, we observed differences even in the type of association between each environmental descriptor and functional trait of tadpoles depending on the waterbody type. It is interesting to notice that, despite the evident differences in terms of functional traits, the species composition in these two systems was similar. The relatively large number of shared species between ponds and streams suggests that the effects of environmental filters on the communities are less prone to be detected based on a taxonomical evaluation (species composition). This reinforces the relevance of a functional approach in a search for ecological differences between communities. In addition, the effect of environmental components on individual variations within the same species would reveal another source of variation in response to habitat, which is another aspect worth investigating (Jordani et al. 2019). The functional approach allowed us to compare communities from a broader ecological perspective. Nevertheless, a combination of functional traits with the natural history of species could be another interesting point for future studies. One possible approach is to analyze how functional traits vary among species that lay eggs exclusively in rivers (*e.g.*, *Boana curupi* and *Crossodactylus schmidti*; Carrizo 1991; Caldart et al. 2014) and ponds (*Elachistocleis*, *Proceratophrys* and *Lithobates;* Rodrigues et al. 2003; Both 2012). This comparison would be interesting since reproductive mode is a potential driver for many ecological adjustments. We could imagine a scenario where behavioral and ecological traits play a complex and complementary role along the anuran life cycle, in which adults exhibit behavioral traits related to their ability to select the correct waterbody for egg laying (river or pond), and larvae with morphological traits related to the ability to survive in each of these waterbodies.

Our data showed that, in ponds, water depth was associated with many functional traits, being, for example, positively associated with the dorsal height of the tail fin. Since fin height contributes to displacement in the water column (Johnson et al. 2015; Jordani et al. 2019), this would be an important factor, especially for nektonic species (*e.g.*, *Dendropsophus* and *Scinax*), favoring the use of different resources in the water column (Marques and Nomura 2018). The relationship between water depth and functional traits deserves attention since the functional diversity of tadpoles tends to increase in medium depths, suggesting that it is surrounded by a complex set of ecological interactions (Queiroz et al. 2015). In temporary ponds, water depth reflects their hydroperiod, which is a limiting factor for tadpole survival (Jordani et al. 2017; Meyer et al. 2020). The speed at which temporary ponds dry defines the time available for metamorphosis, and, usually, the duration affects the size of the newly metamorphosed (Wellborn et al. 1996; Babbitt et al. 2003; Johnson et al. 2015). Another aspect is that, usually, ponds that dry completely are unable to maintain fishes, in particular predators of tadpoles (Wellborn et al. 1996; Werner et al. 2007). The presence of predators has a well-documented effect on tadpole communities, affecting microhabitat selection and morphology. There are indications, for example, that an increase in tail height may be a result of predation pressure (McCollum and Leimberger 1997; Relyea 2003; Relyea and Hoverman 2003). Although a little speculative, we were able to establish a direct relationship between water depth, hydroperiod, metamorphosis, and predation risk (see Simpkins et al. 2013; Melo et al. 2018). Based on this, predation risk (or predation pressure) could be a driver for the detected association between water depth and morphology of the eyes (predator detection), tail (escape ability), and body size (susceptibility to predation). However, associating morphology with a particular environmental factor is a complex and risky task (Lopes et al. 2020), especially in terms of predation since many variables affect it, such as the presence of vegetation or other structures that offer refuge availability (Diaz-Paniagua 1987; Kopp et al. 2006). Other evaluated local variables, such as pH, water conductivity, and presence of arboreal vegetation were associated with functional traits of the nostrils, spiracle, eyes, and tail morphology. Whereas the position of the eyes would be related to habitat evaluation (Johnson et al. 2015; Queiroz et al. 2015; Jordani et al. 2019), nostrils would be related to the circulation of water in the body and assisting with the chemical perception of molecules dissolved in water (Altig and Johnston 1989; Jordani et al. 2019). In fact, chemical perception is a vital ability since the physicochemical components of water may affect the physiology and development of tadpoles. Low pH values, for example, may affect tadpole growth (Pierce 1985; Farquharson et al. 2016; Meyer et al. 2020), and water conductivity, in turn, is related to the susceptibility to diseases (*e.g.*, bacteria and the fungus *Batrachochytrium denbrobatidis*; Carey 1993; Klaver et al. 2013). It is interesting to notice that the physical and chemical descriptors of water were more relevant for stream communities than for pond communities. In streams, functional traits were associated with a larger set of descriptors, such as pH, temperature, conductivity, total alkalinity, Alk, and HCO3. Unfortunately, we have no solid basis to discuss why water proprieties were more relevant for stream than for pond communities. However, it is important to highlight that permanent and unconnected ponds are expected to be more stable environments regarding water parameters than streams. This is expected to be more evident for deeper ones. At the same time, the surrounding environment of ponds and streams has a great potential to change the physical and chemical characteristics of water (Sipaúba-Tavares et al. 2007; Mansano et al. 2012 2014). Although we did not monitor water temperature, this parameter could vary differently between rivers and ponds, thus affecting functional traits. Temperature is one of the main local variables that influence the physical, chemical, and biological processes of streams (Caissie 2006) and can affect tadpole development (see Browne and Edwards 2003), with growth speeding up under ideal temperatures for tadpole growth (Maciel and Juncá 2009).

Our results indicated a possible association in the functional traits related to the physicochemical characteristics of the water and microhabitat used by tadpoles in the waterbodies. This association, highlighted by differences in functional traits between ponds and streams, indicates an ecological response to environmental conditions. These responses can act as an important survival tool in dynamic systems. Since most tadpoles have a short time to complete their metamorphosis, the possibility of quick responses in the face of changes and somewhat unpredictable environmental conditions would be an important tool for the reproductive success of anurans.

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Authors' contributions: R.C.S., D.A.D., D.B., R.K.F., E.M.L. and A.M.T designed the study and wrote the paper. R.C.S. and D.B. collected and processed the data. D.A.D. conducted the statistical analyses. Funding: This research was financially supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Pe. Theobaldo Frantz Fund.

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Availability of data and materials: Data will be made available on request.

Ethics approval consent to participate: All sampling and handling procedures were approved by Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio (Ethical approval ref.: 64962).

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Supplementary materials

Fig. S1. Photographic images showing details of the landscape of each waterbody sampled in the tadpole collection in the areas of Atlantic Forest, in southern Brazil. (download)

Table S1. Tadpole abundance for 28 waterbodies in areas of Atlantic Forest in southern Brazil, recorded from October 2018 to March 2019. P = Pond; S = Stream. (download)

Table S2. Summary of Monte-Carlo tests of RLQ models of ponds. (download)

Table S3. Relationships between pond variables and RLQ axes in the fitted model. (download)

Table S4. Relationship between the tadpole functional traits and RLQ axes in the fitted model of ponds (model with local environmental descriptors). (download)

Table S5. Pond landscape descriptors and RLQ axes. (download)

Table S6. Relationship between the tadpole functional traits and RLQ axes in the fitted model of ponds (model with landscape descriptors). (download)

Table S7. Summary of Monte-Carlo tests of RLQ models of streams. (download)

Table S8. Relationship between the stream local descriptors and RLQ axes of the fitted model. (download)

Table S9. The relationship between tadpole functional traits and RLQ axes of the fitted model which included tadpoles in streams. (download)

Table S10. Relationship between the stream landscape descriptors and RLQ axes of the fitted model. (download)

Table S11. Relationship between the tadpole functional traits and RLQ axes in the fitted model of streams (model with landscape descriptors). (download)