




Growing a fin: wetland and upland effects on tadpole morphology of *Scinax squalirostris* (Anura: Hylidae)

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Abstract

Geographical patterns of phenotypic variation are the outcome of a complex array of evolutionary and environmental factors. Studies on the correlates of the geographic variation in morphological characters can be useful to understand the drivers of phenotypic differences and because intraspecific variation in morphology can impact either local adaptation of any given species or higher-level ecosystem processes. The morphology of larval amphibians responds to multiple factors, including wetland level and surrounding land use. However, understanding the relative influence of such environmental factors on the morphology of tadpoles remains challenging. We used geometric morphometrics to describe the intraspecific morphological variation in tadpoles of *Scinax squalirostris* (Anura: Hylidae) in freshwater wetlands ranging along the transition between the Pampa and Atlantic Forest biomes in southern Brazil. Specifically, we assessed the relative influence of spatial and environmental (aquatic predators, water chemistry and hydroperiod, crop area) factors to tadpole body size and shape. The size of *S. squalirostris* tadpoles was affected by spatial factors and pH. Smaller-sized tadpoles were observed in the Pampa–Atlantic Forest transition. Allometry-free changes in the shape of tadpoles were associated both to wetland and upland factors. Tadpoles in larger ponds showed globular bodies and higher ventral fins, while tadpoles in ponds with higher electrical conductivity showed smaller tails. Tadpoles in ponds surrounded by larger crop areas showed longer fins. Our results are useful to understand the importance of wetland and upland effects on the morphology of widely distributed aquatic species, especially given the ongoing scenarios of land cover modification and climate change.

Keywords Amphibian · Body shape · Body size · Geometric morphometrics · Phenotypic variation · Land use

Introduction

Widely distributed species usually show considerable phenotypic variation within their range. These spatial patterns of intraspecific variation reflect, in brief, the role of adaptive and evolutionary processes (Armbruster and Schwaegerle 1996). In this context, environmental factors are usually considered as important drivers of the geographic variation in the morphology of organisms, because several species manifest different phenotypes at sites with different environmental conditions (e.g., biotic and abiotic factors; Van Buskirk et al. 1997; Verberk et al. 2021; Verberk et al. 2021). Such correlations between environmental factors and phenotypic differences are indicative of the role of local adaptation by means of natural selection or phenotypic plasticity (Travis 1994; Van Buskirk 2009; Perez and Monteiro 2009), although distinguishing between those mechanisms is tricky without accounting for genetic data (Travis 1994;

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Perez et al. 2009; de Abreu et al. 2018). Geographic patterns of phenotypic differences may be unrelated to environmental factors and arise as a result of neutral processes such as genetic drift (Lande 1976; Thorpe 1987; Armbruster and Schwaegerle 1996; Perez et al. 2009). Under the influence of cumulative, random genetic variation over time, one could expect higher morphological dissimilarity among more distant locations due to limited connectivity among spatially isolated sites and, in turn, greater morphological similarity among neighboring populations due to higher gene flow among closer sites, characterizing a pattern of isolation by distance (Wright 1943; Barbujani 1987), where spatial factors (e.g., geographic distances among sites) would be correlated with phenotypic differences. However, identifying the evolutionary processes underlying the spatial variation in phenotype is challenging because they may show complex and interacting effects (Sun et al. 2013; Engen and Sæther 2016; Lee et al. 2016).

The morphology of an organism affects several aspects of its life history (e.g., from growth pattern to reproductive success) and is thus key to its fitness (Arnold 1983). Besides the adaptive consequences for any given species, intraspecific variation in the morphology of specimens can eventually affect other levels of biological organization (e.g., community structure and ecosystem functions) (Bolnick et al. 2011). This holds especially important for species inhabiting freshwater ecosystems such as wetlands. For instance, aquatic larval stages of amphibians (tadpoles) inhabiting wetlands are involved in important ecological processes in these ecosystems, such as nutrient cycling (Montaña et al. 2019). Moreover, earlier studies showed that the ecological roles of tadpoles are mediated by their morphological traits over their development (Schiesari et al. 2009; Ghiocci-Robrecht and Smith 2011; Schriever and Williams 2013), indicating that intraspecific variation in tadpole morphology can ultimately affect the ecological functioning of wetlands.

For example, many authors described morphological responses of tadpoles following changes in hydroperiod duration as a mean to adapt to pond drying (Székely et al. 2010; Amburgey et al. 2012; Brannelly et al. 2019). Decreasing hydroperiod duration can induce shallower body shapes, reduced body sizes and better tadpole swimming performance (Johansson et al. 2010; Székely et al. 2010). Likewise, changes in developmental and behavioral traits to reduce the risk of predation were evidenced in response to predator presence (Skelly and Werner 1990; Wellborn et al. 1996; Anholt et al. 2000; Nunes et al. 2014). Other induced phenotypic modifications in tadpoles may also be the result of inter- and counteracting factors linked to wetland habitat heterogeneity (e.g., area, water depth, vegetation structure, and water chemistry; Grözinger et al. 2014; Johnson et al. 2015; Boelter et al. 2020; Eterovick et al. 2020a; Lopes et al. 2020). For instance, water chemistry factors (e.g., pH,

nitrate, ammonium) of wetlands may affect tadpole development and size at metamorphosis (Gerlanc and Kaufman 2005; Grözinger et al. 2014). Among the water chemistry factors, pH stands out as one of the important factors affecting tadpole development. Specifically, low pH values have been associated with decreased growth of tadpole stages from various species (Brodman et al. 2003). However, most findings on the effect of pH on tadpole morphology stem from laboratory settings (Freda 1986; Anderson and Johnson 2012; Wijethunga et al. 2015), while research on the relationship between pH and tadpole morphology using field-based data is limited and not well established. Most of those abiotic and biotic environmental factors that may influence tadpole morphology are often affected by the hydroperiod gradient of wetlands (Wellborn et al. 1996). However, faster larval development in response to environmental stressors reduces survival of tadpoles and post-metamorphic specimens (Amburgey et al. 2016; Brannelly et al. 2019). Because larval growth, development and size at which tadpoles metamorphose are not necessarily correlated (Relyea 2007; Amburgey et al. 2012), morphological trade-offs across hydroperiods are not intuitive.

In addition, the ecological functioning of small wetlands is closely bound to their surrounding terrestrial habitats, thus the expansion of urban and agro-industrial activities strongly interacts with the ecological conditions of most near-shore habitats (Paerl et al. 2014). In relation to freshwater wetlands, these include many relevant negative effects associated with water quality, altered hydrology and energy flow (Moreira and Maltchik 2015; Moorman et al. 2017; Ji et al. 2018). Natural land cover and human land uses could therefore likely affect habitat suitability to amphibian species and eventually affect tadpole morphology, depending on adult reproductive mode and tadpole plasticity (Becker et al. 2010; Moreira et al. 2020). For instance, land use has been associated with variation in morphological traits of tadpoles, with tadpoles in wetlands surrounded by less-intensive land use showing larger bodies and larger tails (Costa and Nomura 2016; Marques et al. 2019). In coastal areas of southern Brazil, subtropical grasslands are gradually replaced by moist broadleaf forests (Projeto MapBiomias 2020). Along this grassland-forest transition, the spatial arrangement of wetlands was associated with the distribution of tadpole species (Knauth et al. 2019), but spatially structured environmental factors, such as land use and wetland level (water chemistry, hydro-period and pond area), had also distinct influences on tadpole distribution in each biome (Knauth et al. 2019; Moreira et al. 2020). In this context, identifying the most important factors associated with the geographic patterns of phenotypic variation of tadpoles is particularly challenging. Whether land use and wetland characteristics have similar effects on tadpole development,

along their distribution, is subject to discussion. Given the above, studying the morphological variation within the range of a given species and teasing apart the relative importance of spatial and environmental factors can contribute to understanding of how the local environment induce phenotypic changes over a species' development as well as the potential impacts of landscape modifications (Diaz et al. 1998; McGill et al. 2006). In particular, this is important in Neotropical freshwater habitats, which are under increasing pressure by land use change (Mello et al. 2020). Specially, wetland environments are subject to substantial urban and agricultural expansion (Silva and Tagliani 2012). However, most studies on the drivers of morphology of Neotropical tadpoles focus cross-species assessments (Marques and Nomura 2015; Costa et al. 2017; Marques et al. 2019), while intraspecific-level studies focusing widely distributed anurans are rare or spatially restricted (Quinzio and Goldberg 2021).

In this study, we assessed the geographical patterns of intraspecific variation in tadpole morphology of *Scinax squalirostris* (Anura: Hylidae) in wetlands ranging along the transition between the Pampa and Atlantic Forest biomes in southern Brazil. Specifically, we investigated whether tadpole body size and shape change with spatial and environmental factors. We further investigated the relative influence of wetland level (i.e., water-level variables; e.g., predators, water chemistry, wetland area and hydroperiod) and upland factors (i.e., surrounding land use; e.g., crop area) on tadpole morphology when controlling for spatial factors. For the present work, we considered that (i) tadpole morphology strongly responds to local biotic and abiotic factors (Van Buskirk et al. 1997; Van Buskirk 2009; Marques and Nomura 2015; Marques et al. 2019; Boelter et al. 2020); and (ii) that the geographical distribution of wetlands and spatially structured local environmental variables were found to be the main drivers of tadpole distribution in the study area (Knauth et al. 2019; Moreira et al. 2020). Specifically, we tested: (i) whether amphibian populations track the wetland geographical distribution in the study area, i.e., whether phenotype variation of tadpole populations are morphologically more similar among closer wetlands and coarsely follow an isolation-by-distance pattern (Wright 1943) or (ii) whether they are more strongly structured by local adaptation processes resulting from the high environmental heterogeneity of the wetlands. In relation to the effect of wetland- and upland-level factors on tadpole morphology, additionally, we expected that tadpoles inhabiting smaller and more acidic ponds would have smaller body sizes, narrower fins and shorter tails, because increased pH is commonly associated with faster development and metamorphosis in tadpoles (Gerlanc and Kaufman 2005). In addition, tadpoles inhabiting ponds surrounded by smaller crop areas would have larger

body sizes than larger crop areas (Costa and Nomura 2016; Marques et al. 2019).

Materials and methods

Study area and target species

The study area is located in the southern Brazilian Coastal Plain (states of Santa Catarina and Rio Grande do Sul; Fig. S1), which encompasses various wetland types, such as marshes, coastal lagoons, inland lagoons and estuaries. This region is characterized by a mosaic of grasslands, shrubby vegetation (Restinga) and moist forests (Marques et al. 2015). *Scinax squalirostris* is a small-sized tree frog (<3 cm) with a broad geographic distribution, occurring across south and south-eastern Brazil, Uruguay, Argentina, and Paraguay (Maneyro and Carreira 2012; Haddad et al. 2013). Its nektonic tadpoles inhabit small permanent and temporary wetlands, and larval development takes about two months (Maneyro and Carreira 2012; Eterovick et al. 2020b), tadpoles are semi-transparent, their tails have dark spots, their food is based on suspended matter deposited on the bottom of lakes and small ponds.

Sampling design and data collection

The area of the sampled wetlands ranged from 0.14 to 0.8 ha. The ponds were ~10 km apart from each other, and they were selected on the basis of accessibility (i.e., private landowners willing to participate in the study). In the spring of 2015, we sampled tadpoles twice (September and November) in 19 freshwater wetlands across the transition zone between the Pampa and Atlantic Forest biomes (Figs. S1, S2). Samples were taken by dip-netting (30 cm wide, 250 µm mesh size) and sampling effort was 12 sweeps (~1 m²) per sampling wetland, haphazardly distributed across the representative microhabitats in the wetlands (from the margin up to 4 m). Tadpoles were anesthetized with clove oil solution and preserved in the field.

We also assessed the abundance of potential predators of tadpoles in each wetland (Table S2). Taking into account previous studies that recorded tadpoles as their prey items (Kopp and Eterovick 2006; Gambale et al. 2014), we recorded the abundance of families from the following aquatic insect orders: dragonfly (Odonata), giant water bugs (Hemiptera) and adult beetles (Coleoptera). Aquatic insects were sampled using a 30 cm wide entomological net (frame dip-net) with 250-µm diameter mesh. Each sample was represented by a 1-m sweep. We also recorded the presence of fishes in the studied wetlands (Knauth et al. 2019; Bacca et al. 2021). In specific, small individuals (± 3 cm) of five fish families were observed in the ponds: Poeciliidae

(*Phalloceros caudimaculatus*), Callichthyidae (*Corydoras paleatus*), Characidae (*Astyanax* cf. *eigenmanniorum*, *Hyphessobrycon boulengeri*, *Hyphessobrycon* aff. *igneus*, *Mimagoniates inequalis*, *Cheirodon interruptus*), Erythrinidae (*Hoplias* aff. *malabaricus*) and Curimatidae (*Cyphocharax voga*) (Lanés L., personal communication).

In each wetland, we used five environmental variables to characterize local habitat structure: area, pH, electrical conductivity, water turbidity, and hydroperiod. We measured wetland area in situ with a global positioning system device. Water chemistry variables were assessed with a water quality meter (HORIBA U-22). Hydroperiod was assessed based on the monitoring of water availability in each wetland during the sampling period (i.e., between the two sampling events). Wetlands were assigned into two categories: 'long-' or 'short-hydroperiod'. 'Short-hydroperiod' wetlands were those that had either a reduction up to 80% of their surface flooding area or dried up completely between the sampling events, while 'long-hydroperiod' wetlands were those that retained no less than 80% of their original surface flooding area in comparison with the first sampling event.

We defined circular buffers (1000-m radius) and measured agricultural land-cover data (Table S1) using Qgis (ver. 2.18.16, <https://qgis.org/en/site/>, accessed 10 December 2020). We performed analysis on Google Earth imagery using a land-cover classification for 2015 produced within the scope of the Mapbiomas initiative (Projeto MapBiomas 2020). We focused only area extension agricultural land use because amphibians with aquatic reproductive modes (such as *S. squalirostris*) seem particularly sensible to such habitat modification in the study area (Moreira et al. 2020).

Geometric morphometric analysis

Only specimens between Gosner's stages 31 and 37 were used for morphometric analyses to ensure comparable sizes across sites (Fig. S3). Specimens with damaged tails were excluded. Analyses of shape and size were derived from 71 tadpole specimens of *Scinax squalirostris*: 32 in

the Pampa (number of individuals per wetland ranging from two to six), and 39 in the Atlantic Forest (number of individuals per wetland ranging from one to 11).

We took digital images of lateral view for each specimen using a digital camera (Canon Rebel T5i; 150 mm lens) mounted to a copy stand. A set of 13 landmarks was digitized from each image in according to Van Buskirk (2009) with some minor modifications: (Fig. 1): (1) most anterior point of the body; (2) nostril; (3) the center of the eye; (4) most lateral point of the eye; (5) dorsal fin origin; (6) tip of the tail; (7) most anterior point of the proctodeal tube–ventral fin junction; (8) maximum ventral curvature of the body; (10) most anterior point of the oral disk–body junction; (11) most dorsal point of the caudal musculature–body junction; (12) most anterior point of the axis of the tail myotomes (13) most ventral point of the caudal musculature–body junction. Ten semilandmarks were set to capture shape and were positioned between landmarks. Three semilandmarks are positioned between points 5 and 6, 7 and 6 and two semilandmarks between points 11 and 6, 13 and 6.

The configuration of landmarks and semi-landmarks was then digitized using tpsDig2 software, version 2.16 (Rohlf 2010). After digitization, we applied a Generalized Procrustes Analysis (GPA) in the matrices of coordinates to standardize the size and align the configuration of landmark coordinates. Such approach enabled us to separate differences among landmarks configuration in two components—size (as centroid size) and shape (as GPA residuals) (Rohlf and Slice 1990; Cordeiro-Estrela et al. 2006). We ran a multivariate regression analysis using the *geomorph* package (Adams et al. 2019) to test for the presence of allometry in the sample. Because the relationship was significant ($P=0.001$), with size predicting about 12% of shape variation, we used the residuals of the regression of shape on size instead of original data. The resulting allometry-corrected data were then subjected to a principal component analysis (PCA) and PCA scores were used in all further analysis.

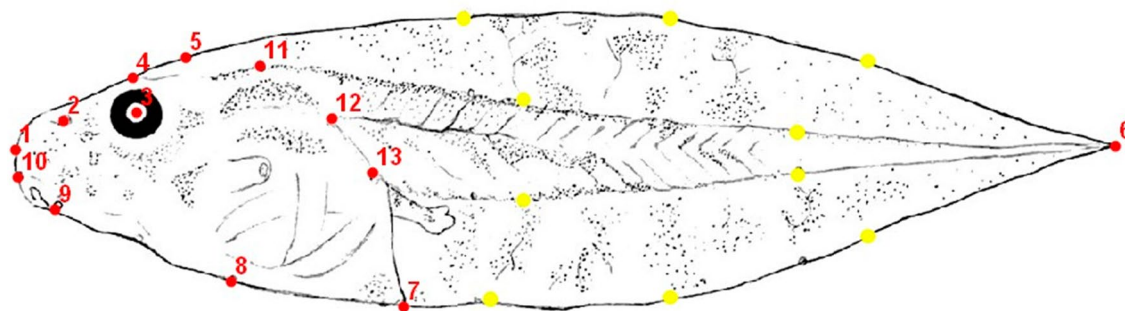


Fig. 1 Position of the 13 landmarks (red circle) and 10 semilandmarks (yellow circle) in a lateral view of the *Scinax squalirostris* tadpole

Data analysis

To account spatial autocorrelation in size, we estimated Moran's correlogram based on five distance classes. As positive autocorrelation was detected, we used a distance-based Moran's eigenvector map (dbMEM) analysis (Dray et al. 2006). We retained one MEM modeling broad spatial scales that correspond to the spatial filter used in the subsequent analysis to eliminate spatial autocorrelation. We assessed the relationship between tadpole size and environmental variables using linear models (including spatial filter in all models) with forward selection based on AICc model selection criteria. Linear models and spatial analyses were run in R 4.1.1 (R Core Team 2020) using the *adespatial* package (Dray et al. 2020).

Relationship between tadpole shape and environment was tested using a partial redundancy analysis (RDA) controlling for spatial structure (here represented by MEM variable as previously described). Before modeling, we analyzed the multicollinearity structure among predictors using the variance inflation factor (VIF). However, all VIF values were <5 and our final analyses were performed with the seven predictors. As our global model with all predictors was significant ($P=0.001$), we proceeded with a forward selection of variables on the basis of adjusted R^2 and significance of each explanatory variable (Blanchet et al. 2008). We created graphical representations of shape change (relative to average shape) based on partial least squares analysis-PLS (Fruciano et al. 2011). Predicted shapes were obtained with two-block PLS using shape variables as first block, and as second block of variables, the same environmental variables present in the final RDA (scaled to unit variance). We also ran separate PLS for each environmental variable used in the RDA, using the *geomorph* and *Morpho* (Schlager 2017) packages in R.

Results

The best model explaining the size *S. squalirostris* tadpoles included spatial filters and pH (Table 1). Together, they explained 20% of the variation in tadpole size, with negative

Table 1 Effects of environmental factors on body size of tadpoles of *Scinax squalirostris* indicate a negative relationship

Model	AICc	Δ AICc	Adj R^2
MEM, – pH	2042.3	0	0.20
MEM, – pH, – predators	2044	1.9	
MEM, –pH, – predators, area	2046.1	4.0	
MEM, –pH, – predators, wetland area, crop area	2048.4	6.3	

association for pH values and positive for spatial structure (MEM). Spatial filter (MEM) explained 13% of the variation in size, while the joint contribution between pH and MEM explained the remaining fraction. Small-size tadpoles were associated to small values of MEM, indicating that individuals from wetlands in the Pampa–Atlantic Forest boundary had smaller sizes (Fig. 2).

The forward selection procedure retained three variables in the final model and four variables were not included (pH, water turbidity, hydroperiod, and predators). After controlling for spatial correlation, there was a weak but significant ($F_{3,66}=2.789$; $P=0.001$) association between shape and environmental variables (Table S3). Wetland area, electrical conductivity, and crop area explained 10.9% of the variation in the shape (Table 2). Shape changes predicted (first PLS axis) by the association of shape and environmental variables are showed in Fig. 3A. Separate PLS of tadpole shape were significant for all three variables (Table S4). Individuals from small wetlands have body depressed and ventral fin low with margin parallel to the longitudinal tail axis, while individuals from large wetlands have body globular and ventral fin high, with a convex margin (Fig. 3B). Tadpoles from wetlands with high electrical conductivity have body globular and small tail (Fig. 3C). Individual from ponds without surrounding crop area has shape similar to reference shape, while tadpoles from crop areas have larger fins (Fig. 3D).

Discussion

We assessed the geographic patterns and the ecological correlates of the intraspecific morphological variation of *S. squalirostris* tadpoles in coastal wetlands ranging along a grassland–forest transition in southern Brazil. Model selection procedures showed that broad-scale spatial factors along with wetland (water level) and upland environmental factors were jointly important to explain variation in both tadpole shape and size in the study area. Assuming that an association between geographic patterns of phenotypic variation and spatial factors could be a signature of isolation-by-distance process, while phenotype–environment correlations, of adaptive processes (Wright 1943; Van Buskirk et al. 1997; Perez et al. 2009; de Abreu et al. 2018), we found basic support for the two main hypotheses being tested.

However, one major result is that the relationships between the traits and correlates assessed remarkably differed: while body size was better explained by broad-scale spatial filter (MEM), followed by the joint contribution of MEM and pH, shape was better predicted by wetland-level and upland environmental factors, seconded by MEM. Thus, a closer look at our findings suggests a complex interplay of the geographical distribution of the wetlands and local adaptation processes in shaping tadpole morphology in the

Fig. 2 Distance-based Moran's eigenvector map (MEM) describing broad-scale spatial autocorrelation of the *Scinax squalirostris* tadpole size. Increasing size of the symbols corresponds to increasing positive values, in black, and increasing negative values, in white, of the eigenvector. Wetlands with the same color show similarity in tadpole's size and the size of the symbols indicates the level of similarity; small symbols stand for low similarity, large symbols stand for high similarity

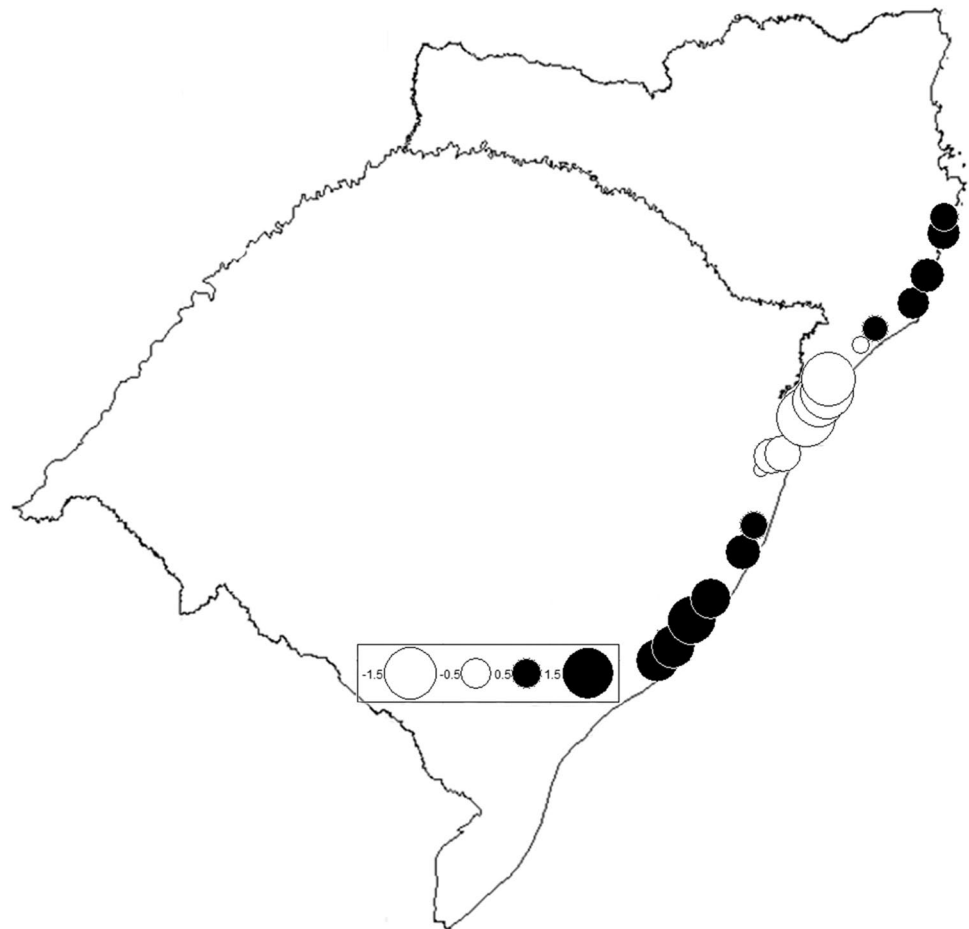


Table 2 Results of partial redundancy analysis (RDA) describing the relationship between environmental variables (controlling for spatial correlation) and shape of *Scinax squalirostris* tadpoles

P (full model)	Adj R^2 (full model)	Variable	P	Adj R^2
0.001	0.167	Wetland area	0.02	0.11
		Conductivity		
		Crop area		

Full model includes predators, wetland area, hydroperiod, water turbidity, pH, electrical conductivity, and crop area

region. Although there is evidence for complex and interacting effects of spatial and environmental factors underlying phenotypic variation for other taxa (Sun et al. 2013; Engen and Sæther 2016; Lee et al. 2016; de Abreu et al. 2018), we unraveled patterns of intraspecific phenotypic variation and the roles of ecological correlates to a spatial extent usually not considered in studies focusing wetland amphibians in the Neotropical region (Goldberg et al. 2018; Marques et al. 2019; Quinzio and Goldberg 2021).

Variation in tadpole body size was predominantly explained by the broad spatial filter (MEM1). Although

it indicates that geographically closer wetlands harbored tadpole populations morphologically more similar in terms of body size (suggesting isolation by distance), the relationship between body size and wetland location was not linear across the study area. Specifically, tadpoles with smaller sizes were associated with wetlands located in the Pampa–Atlantic Forest boundary, while tadpoles with larger sizes were found at the northern and southernmost parts of the study area. The predominance of the broadest spatial filter agrees with previous studies stressing the role of broad-scale spatial factors on the distribution of aquatic taxa (e.g., amphibian and aquatic insects) in coastal wetlands ranging along the transition zone between Atlantic Forest and Pampa (Pires et al. 2018; Knauth et al. 2019; Bacca et al. 2021). In this context, the importance of the broad spatial filter for tadpole size is discussed considering the knowledge on amphibian biology, as well as the limitation of our approach. As for the latter, we lack genetic data to investigate the potential role of genetic similarity (Barbujani 1987; Perez et al. 2009) or movement information underlying the spatial structure (Sinsch 2014) among these morphologically alike subpopulations, we highlight that our proposed explanation is yet tentative.

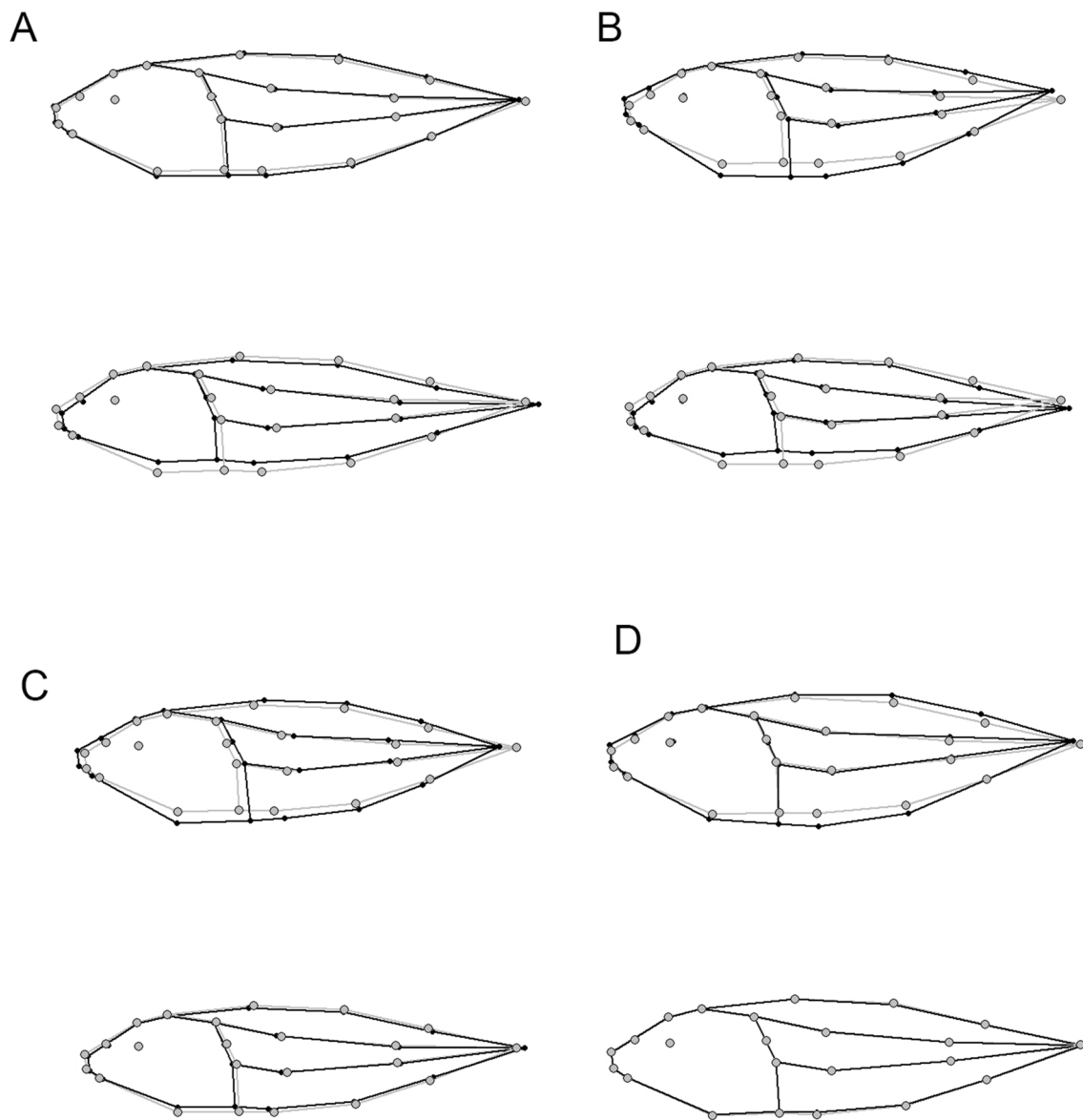


Fig. 3 Shape changes predicted by partial least square analysis: **A** all environmental variables, **B** wetland area, **C** electrical conductivity, **D** crop area. Gray outline corresponds to the average form. Black out-

line corresponds to negative extreme (bottom) and positive extreme (top), respectively

As for the former, variation in body size could be explained by a potential role of local climatic features underlying hydric regime of each wetland. In specific, along the extent of the study area, there is a strong variation in precipitation and temperature (Alvares et al. 2013). These variables can strongly drive local hydroperiod through flood and evaporation regimes (Jackson et al. 2014) and thus drive larval growth, ultimately affecting body size (Brannelly et al. 2019). A recent study assessing adults from a sister species (*S. fuscovarius* (A. Lutz, 1925)) detected changes in body sizes among drier and humid areas (Goldberg et al. 2018). Another potential explanation for the importance of

the broad spatial filter to tadpole size is likely associated with the role of biome type, since MEM1 summarized the transition between the Atlantic Forest and Pampa biomes. On this matter, the study of Knauth et al. (2019) showed that the relative importance of local environmental variables on tadpole distribution varied in each biome. In specific, water chemistry, hydroperiod and pond area were important structure amphibian distribution in the Atlantic Forest, whereas water chemistry features seem to be the sole factor in the Pampa. Specifically, it fits well with a potential effect of the turnover on the relative magnitude of abiotic and biotic interactions on tadpole phenotype in each biome.

In addition, body size was influenced by joint fraction of pH and the broad spatial filter, suggesting the influence of local adaptive processes coupled with geography. The heterogeneous spatial distribution of amphibian phenotypes associated with the transition between the Pampa and Atlantic Forest biomes and wetland and upland environmental factors resembles previous studies showing that patterns of phenotypic variation in anuran larvae is spatially-dependent (Michel 2011). As for water chemistry variables, there are several reports showing effects of pH on development, locomotion, and mortality of tadpoles (Barth and Wilson 2010; Thabah et al. 2018). The growth deceleration prior to metamorphosis and early emergence at a small size is widespread among amphibian families (Székely et al. 2017; Brannelly et al. 2019; Mogali et al. 2021).

Shape variation in *S. squalirostris* tadpoles appeared to be consistent with our expectations. Specifically, the variation in tadpole shape was related to wetland pH, area, conductivity and crop area at a 1000-m radius. Because size predicted about 12% of shape variation in our data, environmental factors affecting tadpole sizes may have consequences for general shape through allometric shape variation. However, it is important bear in mind that our results of shape changes were allometry-free. In general, tadpoles inhabiting small ponds had depressed bodies and lower ventral fins. We were unable to identify why shallower body shape seems to be an adaptive response to water-level conditions; however, such shape responses were been found for other species under scenarios of hydrological stress (Tejedo and Reques 1994; Richter-Boix et al. 2006; Johansson et al. 2010). It is important to recognize that a depressed body jointly with elongated and finless tail: (i) has better swimming performance; (ii) can be reabsorbed faster by tadpoles; (iii) may become obsolete in shallow-water conditions (Van Buskirk and Saxer 2001; Richter-Boix et al. 2006; Johansson et al. 2010). As ponds become shallower/smaller, tadpole's likely face more crowded conditions, which in turn would increase predation rates as well as intra- and interspecific competition. Such density-dependent changes linked to hydroperiod are major factors that induce variations in morphology in larval amphibians (Tejedo and Reques 1994; Rogers and Chalcraft 2008; Schalk 2016). In this study, predatory fish and invertebrate predators occurred in all ponds. We did not assess larval density and to predation we considered only the abundance of aquatic insects as potential predators, but one could expect that the regional species pool be filtered in different local assemblages.

In addition, tadpole shape is the result of multiple processes occurring at different scales that can result in similar shape patterns or shift associated with antagonistic effects. Behavior and morphology are individual characteristics that can be affected by various anthropogenic factors in organisms such as larval amphibians (Marques et al. 2019), e.g.,

land use. Here, tadpoles from ponds surrounded by smaller crop areas bore superficial resemblance to their reference values, while tadpoles present in ponds with larger crop areas showed larger fins, demonstrating that these organisms, according to changes in land use around the ponds, have the ability to adjust their morphology. While agricultural runoff has strong teratogenic and genotoxic effects on tadpoles (Mann et al. 2009; Silva et al. 2021), the water availability associated with land preparation and crop cycle can be particularly challenging for amphibians in agricultural landscapes (Moreira and Maltchik 2014; Schiesari and Corrêa 2016). These stressors can influence behavioral and morphological changes in the individual traits of organisms. There is evidence that in ponds surrounded agricultural land use, the invasion of predators and competitors can be facilitated (Blann et al. 2009). Interestingly, a significant relationship between agricultural activities and morphological changes associated with eye position and fluctuating asymmetry is previously reported for Neotropical tadpoles (Costa and Nomura 2016; Marques et al. 2019). Deep tail fins act as bait, preventing deadly blows to the body wall (Johnson et al. 2015). During larval development, exposure to predation risk induces the expression of defenses, some species of amphibians are able to recognize predator's cues, whether visual, physical or chemical (Nunes et al. 2014).

Conclusion

The morphology of *S. squalirostris* tadpoles was influenced by a combination of spatial factors, wetland-level (biotic and abiotic factors) and land use environmental factors in subtropical coastal wetlands in southern Brazil. Our results suggest a complex interplay of geographical and local adaptive processes shaping tadpole phenotypes in the study area. Although we lack genetic data to further untangle the roles of selection and phenotypic plasticity in driving the observed patterns of intraspecific variation in tadpole morphology (Travis 1994; Armbruster and Schwaegerle 1996; Perez and Monteiro 2009; de Abreu et al. 2018), our finding agrees with the general view that tadpole morphology is highly responsive to environmental conditions (Van Buskirk et al. 1997; Van Buskirk 2009; Marques et al. 2019; Boelter et al. 2020). In this regard, future approaches that include genetic data might be particularly instructive to further untangle the roles of connectivity among wetlands and phenotypic plasticity in driving the observed patterns of intraspecific variation in tadpole morphology. Additionally, sampling at other seasons would allow testing of the roles of the seasonal change in local environmental factors on the morphology of tadpoles.

Nonetheless, given the lack of genetic data on the target species, we stress that our proposed explanation is tentative,

yet potentially informative. Furthermore, after controlling for spatial correlation, we showed that tadpole morphology of *S. squalirostris* is affected by water-level and surrounding land use environmental factors in similar magnitude. Because future scenarios of land cover modification and climate change are predicted to result in ponds drying earlier and staying drying longer, our results can provide insights with respect to the potential effects of those drivers on other wetland-dwelling species with similar ecologies. Moreover, given the important roles that tadpoles play in the ecological processes in wetlands and the knowledge that these roles are mediated by their morphological traits, our findings are important to understand the impact of land use and water-level environmental changes in the ecological functioning of such ecosystems.

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Author contributions TB: Conceptualization, Formal analysis, Data curation, Methodology, Visualization, Writing – original draft, Writing – review & editing. LFBM: Formal analysis, Visualization, Validation, Writing – review & editing. MMP: Methodology, Visualization, Writing – review & editing. CS and LM: Funding acquisition, Project administration, Supervision, Writing – review & editing.

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Data availability Specimens are deposited in the collection of the laboratory of UNISINOS.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval We declare that data collection complied with the current Brazilian environmental laws (SISBIO 36365-2).

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