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Macroecology of reproductive modes in the diverse anuran fauna of the Brazilian Atlantic Forest

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Abstract

Macroecology of reproductive modes in the diverse anuran fauna of the Brazilian Atlantic Forest. Anurans exhibit the widest variety of reproductive modes among tetrapod vertebrates. The Atlantic Forest is a hotspot for biological conservation; however, biogeographic documentation of the richness of anuran reproductive modes are underexplored. By overlaying maps of 249 species having reproductive modes with aquatic eggs and 101 species with non-aquatic eggs, we described the geographical patterns of anuran reproductive modes in the Atlantic Forest and identified the main correlates of reproductive diversity of these two major types of anuran reproduction. We found the greatest diversity of reproductive modes in the coastal region of the Atlantic Forest, whereas a smaller number of reproductive modes was found in inland regions of the hotspot. These regions are broadly characterized by deciduous/semideciduous forests and a warmer and more seasonal climate regime in southeastern and southern Brazil. In this climatically harsher region, reproductive modes were more basal and generalized in anurans. Correlative analyses showed that the richness of reproductive modes with aquatic eggs can be described by general combinations of climate, topography, and vegetation types, whereas larger numbers of reproductive modes with non-aquatic eggs are better described by specific variables of temperature seasonality, amount of ombrophilous forests, and rugged topography. The predictors identified here are environmental variables that should be continuously monitored *in situ;* identifying threshold values that could lead a species to a critical conservation status is key to efficiently protecting the rich anuran fauna of the Atlantic Forest.

Keywords: Biogeography, Biological diversity, Neotropical amphibians, Reproductive diversity.

Resumo

Macroecologia dos modos reprodutivos da diversa anurofauna da Mata Atlântica brasileira. Os anuros exibem a maior variedade de modos reprodutivos entre os tetrápodes vertebrados. A Mata Atlântica é um importante *hotspot* para a conservação biológica; no entanto, documentações

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biogeográficas da riqueza de modos reprodutivos de anuros são pouco explorados. Utilizando a sobreposição de mapas de 249 espécies com modos reprodutivos aquáticos e 101 espécies com modos reprodutivos não-aquáticos, nós descrevemos os padrões geográficos dos modos reprodutivos de anuros na Mata Atlântica e identificamos as principais variáveis correlacionadas com a diversidade reprodutiva destes dois maiores tipos de modo reprodutivos. Encontramos uma maior diversidade de modos reprodutivos na região costeira da Mata Atlântica, sendo que um menor número de modos reprodutivos foi encontrado na região interiorana do *hotspot*. Essas regiões são amplamente caracterizadas pela presença de florestas decíduas/semidecíduas em um regime climático mais quente e sazonal na região sudeste e sul do Brasil. Além disso, os poucos modos reprodutivos encontrados nesta região são aqueles considerados mais primitivos e generalizados nos anuros. As análises correlativas mostram que a riqueza de modos reprodutivos com ovos aquáticos está relacionada com combinações gerais de clima, topografia e tipos de vegetação, enquanto que os modos reprodutivos com ovos não-aquáticos são melhores relacionados com variáveis específicas de sazonalidade de temperatura, quantidade de florestas ombrófilas e topografia acidentada. As variáveis identificadas no presente estudo são importantes para serem continuamente monitorados *in situ*, já que a identificação de valores limítrofes de tais preditores que levariam o status de conservação de uma dada espécie para níveis críticos é extremamente importante para a conservação eficiente da rica anurofauna da Mata Atlântica.

Palavras-chave: Anfíbios Neotropicais, Biogeografia, Diversidade biológica, Diversidade reprodutiva.

Introduction

Anurans are the most diverse order of Amphibia with approximately 7,446 species worldwide (Frost 2021). A wealth of adaptations have led anurans to successfully exploit terrestrial and associated freshwater environments; consequently these animals have evolved the greatest reproductive diversity of all tetrapod vertebrates (e.g., Haddad and Prado 2005, Crump 2015, Malagoli *et al.* 2021). Using a combination of traits that includes oviposition sites, ovum and clutch characteristics, rate and duration of development, stage and size of hatchling, and type of parental care, if any (Salthe and Duellman 1973), scientists have identified more than 40 anuran reproductive modes worldwide (Haddad and Prado 2005, Iskandar *et al*. 2014, Kusrini *et al*. 2015, Malagoli *et al*. 2021). Besides elucidating the evolutionary ecology of anurans, the study of reproductive modes assists in biological conservation actions guided by life-history traits related to reproductive requirements (e.g., Loyola *et al.* 2008, Becker *et al.* 2010).

In general, anuran reproductive modes can be split into two major categories (Haddad and Prado 2005): (1) aquatic eggs that are either deposited directly in the water or in aquatic foam nests or bubble nests, or embedded in the dorsum of aquatic females; and (2) terrestrial or arboreal eggs (not in water) that are deposited on the ground, on rocks, or in burrows, as well as on vegetation, associated or not with foam nests, or even carried by adults (on the body of an adult or internally retained in a female oviduct). Additionally, the non-aquatic category includes some species that have direct development of terrestrial eggs, in which the tadpole phase is abbreviated.

The most common reproductive mode is the deposition of eggs and the development of exotrophic tadpoles in lentic water, which is also considered the most basal mode in anurans. Other reproductive modes generally represent a continuum of specializations toward the use of different terrestrial environments (Duellman and Trueb 1994, Haddad and Prado 2005, Crump 2015). Irrespective of whether this trend toward terrestriality exhibits a phylogenetic signal (e.g., Benício *et al*. 2021) or not (e.g., Gomez-Mestre *et al*. 2012, Pereira *et al*. 2015), the evolution of anuran reproductive modes is believed to be a result of repeated independent events of terrestrial breeding strategies from the plesiomorphic fully aquatic breeding (Meegaskumbura *et al*. 2015, Portik and Blackburn 2017). Anurans with non-aquatic eggs still depend on water for reproduction, either for tadpole development or in the form of moist environments for direct development of eggs (Duellman and Trueb 1994). This dependence on water makes these animals highly sensitive to environmental variation from local to regional scales (Werner *et al*. 2007, Rossa-Feres *et al*. 2011, Haddad *et al*. 2013). Various studies have found correlations between species richness (or diversity of reproductive modes) and climatic variables, which are generally attributed to a given trait specialization (e.g., a particular reproductive mode) adapted to a given climatic regime (Vasconcelos *et al*. 2010, Silva *et al*. 2012).

The Atlantic Forest, located along the Brazilian Atlantic coast, is a biodiversity hotspot and the second largest tropical forest in South America (Mittermeier *et al*. 2004). It is home to one of the most diverse anuran faunas in South America (IBGE 2012; Vasconcelos *et al*. 2019), in which anurans exhibit the highest reproductive diversity in the world (Haddad and Prado 2005). Anuran diversity is greatest in the ombrophilous/evergreen forests of the southeastern coastal region (Haddad *et al*. 2013, Vasconcelos *et al*. 2014). Studies focusing on different Atlantic Forest regions (e.g., mostly in southeastern and southern Brazil) found that anuran reproductive diversity is related to taxonomic species richness: larger numbers of reproductive modes occur in more humid forests with rugged topography (Vasconcelos *et al*. 2010, Silva *et al*. 2012, Haddad *et al*. 2013). As described above, anuran reproductive modes can be split into two categories related to their dependence on water: reproductive modes with aquatic eggs and those with non-aquatic eggs. Although most anuran species have an aquatic tadpole phase, species with non-aquatic eggs undergo an embryonic period away from water. Undergoing this critical stage out of water in a dry or humid environment results in differences in survival rates of tadpoles compared to tadpoles of those species that lay eggs in water. We hypothesized that the prevalence of reproductive modes with non-aquatic eggs will be associated with environmental variables such as water or temperature seasonality and that the prevalence of reproductive modes with aquatic eggs will be associated with other variables (e.g., general trends of rainfall or temperature regimes). Our main focus is to elucidate the environmental correlates of these two major categories of reproductive modes in the diverse anuran fauna of the Atlantic Forest.

We mapped reproductive diversity of anurans throughout the Atlantic Forest based on whether a species has an aquatic or non-aquatic reproductive mode. We performed correlative analyses and identified the main correlates of these two major types of reproductive modes. We tested which of the environmental variables (climatic, topographic, and habitat-related variables) were indicative of the type of reproductive mode. We hypothesized that the different types of reproductive modes would have distinct sets of predictors because of their inherent differences in dependence on water. Reproductive modes with aquatic eggs should depend on the accumulated water volume; therefore, we expected that climatic trends such as total annual rainfall and mean annual temperature would be correlates of these modes. Reproductive modes with non-aquatic eggs may not directly depend on accumulated water. A humid environment may be more indicative of the prevalence of these types of reproductive modes. These modes should be correlated with variables associated with climatic or environmental stability such as seasonality in precipitation or temperature and the presence of evergreen forests (e.g., Müller *et al*. 2013).

Material and Methods

Species Data and Study Site

Using the Atlantic Forest species list of anurans compiled by Haddad *et al*. (2013), we downloaded the distribution maps from the IUCN (2017) database and updated the taxonomic nomenclature according to the Amphibian Species of the World database (Frost 2021, updated through January 2020). Anuran species lacking distribution maps in the IUCN (2017) portal (e.g., recently described species) were surveyed using point occurrences to generate their ranges using the minimum convex polygon calculated from the points (e.g., García-Roselló *et al*. 2015, Vasconcelos *et al*. 2019). Species maps with information on reproductive modes were overlapped onto a grid system of the continental Atlantic Forest with resolution of ~50 km (i.e., islands were not considered), allowing generation of a presence/absence matrix of species distributions.

Recently, Nunes-de-Almeida *et al.* (2021) revisited the classification of amphibian reproductive modes and proposed the existence of 71 modes for anurans. Though this classification represents almost twice the number in the classification proposed by Haddad and Prado (2005), we followed the previous classification in this study. Our results are subject to changes under a reanalysis using the classification by Nunes-de-Almeida *et al.* (2021). We believe that such a reanalysis may not result in major changes because some aquatic and non-aquatic reproductive modes proposed by Haddad and Prado (2005) are now divided into new modes, in addition to new modes proposed by Nunes-de-Almeida *et al*. (2021) within both aquatic and non-aquatic categories. Information regarding reproductive modes of each species was taken from Haddad *et al*. (2013), which used the classification by Haddad and Prado (2005). Of the 529 anurans listed by Haddad *et al*. (2013), we compiled distribution maps for 249 species having reproductive modes with aquatic eggs and 101 species with non-aquatic eggs (Appendices I and II). We ignored those species lacking information regarding their reproductive modes, as well as island-endemic species. Many of these species have small ranges and are known only from their type-localities or from a small number of localities (e.g., *Ischnocnema erythromera*, *I. izecksohni*, *Dendrophryniscus proboscideus*, *Frostius erythrophthalmus*, and *Cycloraphus organensis*). Excluding these species is not a critical issue for the present study; according to the niche conservatism hypothesis and the high phylogenetic signal in the reproductive modes of Atlantic Forest anurans (Benício *et al.* 2021), the excluded species are more likely to exhibit the same reproductive modes as other species in the same genus/family, which in turn are already represented by the congeneric species.

Climatic, Topographic, and Habitat-Related Variables

In order to identify the correlates of anuran reproductive diversity, we selected environmental variables that represent potential limits of physiological tolerances for egg development, physical barriers for species distributions, and/or habitat preferences for a given reproductive mode (e.g., Vasconcelos *et al*. 2010, Silva *et al*. 2012, Vasconcelos *et al*. 2014). Mean annual temperature (TEMP), temperature seasonality (TSEASO), annual precipitation (PRECIP), and precipitation seasonality (PRECSEASO) were downloaded from the Chelsa Climate database (Karger *et al.* 2021) at a 1 × 1 km resolution. Annual actual evapotranspiration (AET), which measures the water-energy balance, was downloaded from the Food and Agriculture Organization of the United Nations (FAO: http://www.fao.org/geonetwork/srv/en/metadata.show?id=37233) at a resolution of 10 × 0 km. Topographic heterogeneity (TOPO) was determined using the standard deviation of the mean altitude within each 50 × 50 km grid cell based on the altitude data of 1 × 1 km resolution available at the U. S. Geological Survey portal (https://lta.cr.usgs.gov/GTOPO30). Habitat-related variables were based on how much native forest area is present within a 1 × 1 km resolution. We recognized two forest formations that are predominant in the Atlantic Forest: the deciduous/semideciduous forest (DECIDUOUS) and the ombrophilous forest (also known as EVERGREEN) (Tuanmu and Jetz 2014). For each DECIDUOUS and EVERGREEN map, the grid cell provided information regarding the total area of native forest within this resolution.

Except for the TOPO, which was determined using the standard deviation of the mean altitude of the original layer (1 × 1 km), all explanatory variables were derived from the mean value at each cell of the Atlantic Forest grid system.

Data Analyses

Prior to the analyses, the response (i.e., number of aquatic and non-aquatic reproductive modes) and predictor variables were square root or log transformed to reduce heteroscedasticity and normalize model residuals. The predictor variables were standardized using z-scores to provide comparable regression coefficients (Quinn and Keough 2002).

We performed two approaches to identify the correlates of the reproductive modes: the performance of traditional general linear models (Legendre and Legendre 2012) and spatially explicit simultaneous autoregressive models (SAR; Kissling and Carl 2008). The first approach makes use of ordinary least-squares regression (OLS) that aims to find a straight line that minimizes the sum of squares of the vertical residuals between the observed values and the regression line (Legendre and Legendre 2012). A series of OLS models were performed separately with different sets of predictors for the aquatic and non-aquatic reproductive modes. A model selection was performed based on the Akaike Information Criteria corrected for small samples (AICc) (Burnham and Anderson 2002), of which the model with the lowest AICc was identified as the best model (see similar applications in Boaratti and Silva 2015, Vasconcelos *et al*. 2019). The best models for aquatic and non-aquatic eggs identified by the AICc were also the ones used for the SAR approach.

The second approach, the spatially explicit simultaneous autoregressive models (SAR; Kissling and Carl 2008), was performed because of the presence of spatial autocorrelation in OLS model residuals that violates the assumption of residual independence, which in turn can distort estimates of model parameters. SAR models minimize the effect of spatial autocorrelation and identify the variables that effectively contribute to the richness patterns of the reproductive modes. SAR models are spatially explicit and allow the incorporation of residuals spatially autocorrelated at different classes of errors during the model building. By using spatial correlograms (Moran's *I*), we defined an intermediate value between the first and second class of the spatial correlogram (i.e., alpha = 1.5; neighborhood points separated by 50–100 km) because these were the classes with the highest values of Moran's *I* for aquatic and non-aquatic reproductive modes. OLS, SAR, and the AICc analyses were performed using the software Spatial Analysis in Macroecology (Rangel *et al*. 2010).

Results

Richness Patterns of Reproductive Modes

Reproductive diversity per grid across the Atlantic Forest varied between three and 12 aquatic reproductive modes and between one and 12 non-aquatic reproductive modes (Figure 1). Irrespective of the reproductive mode classification, most reproductive diversity is found along the Atlantic coast, whereas fewer reproductive modes are found in the inland region. This gradient is steeper for the non-aquatic modes (Figure 1).

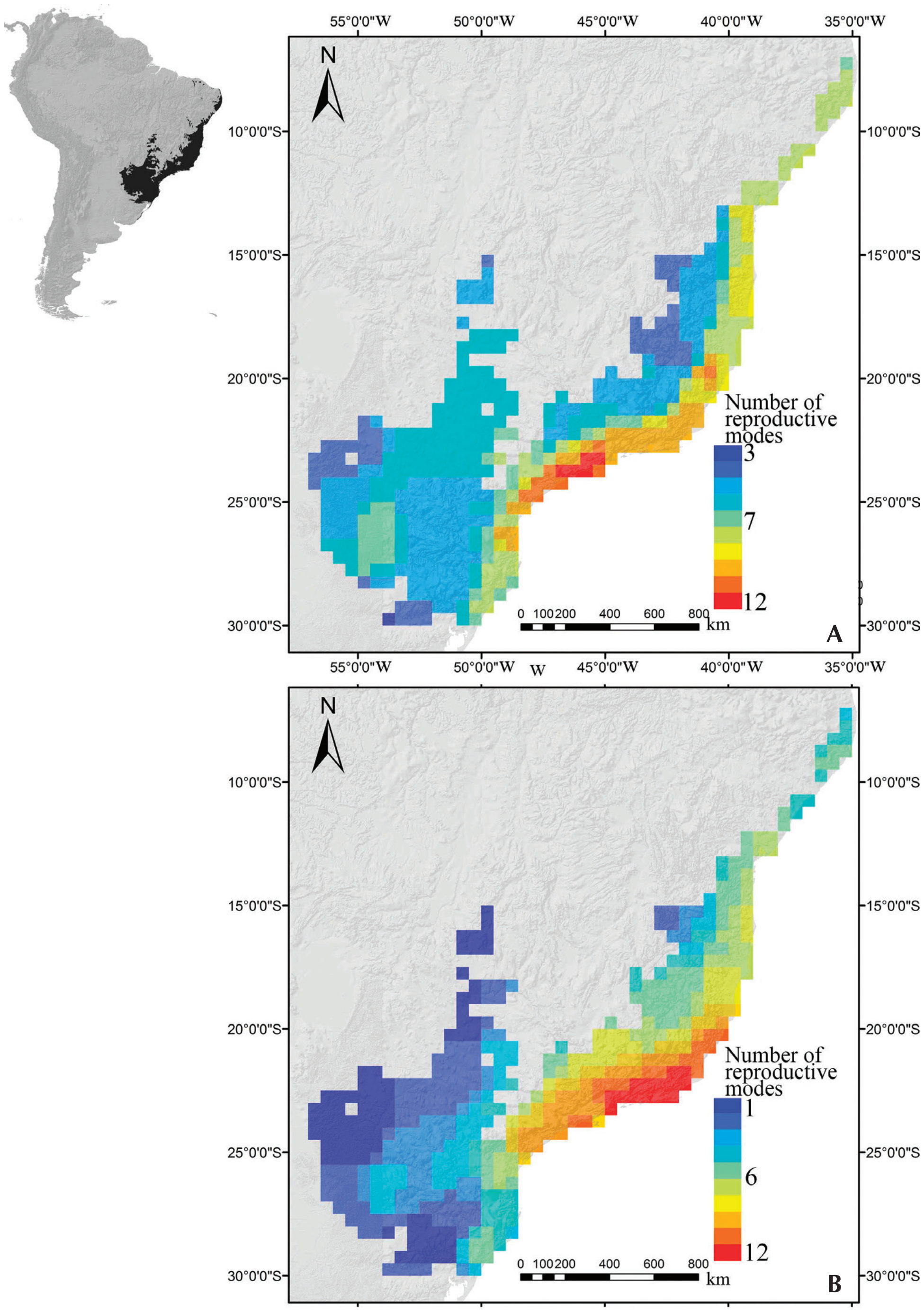

Figure 1. Diversity gradients of the anuran reproductive modes in the Atlantic Forest for the modes having (**A**) aquatic and (**B**) non-aquatic eggs.

Correlates of the Reproductive Modes

OLS models for the aquatic (Table 1) and non-aquatic (Table 2) reproductive modes indicate that the best models have six environmental variables for both categories. The best model of the aquatic reproductive modes (Table 1) includes the climatic variables AET, TSEASO, PRECIP, the topographic variable (TOPO), and the habitat-related variables DECIDUOUS and EVERGREEN. The best model for the non-aquatic reproductive modes (Table 2) includes the climatic variables AET, TEMP, TSEASO, and PSEASO, the topographic variable (TOPO), and the habitat-related variable EVERGREEN.

Regarding the aquatic reproductive modes, the six variables of the OLS (R^2 adj = 0.379, $F = 48.301$, $p < 0.001$) and SAR models (R^2 adj = 0.408, $F = 43.021$, $p < 0.001$) explained relatively similar levels of variance between them. All variables of the OLS and SAR models have significant correlations with the aquatic reproductive modes, except the variable PRECIP for the SAR model (Table 3).

Regarding the non-aquatic reproductive modes, the total variance explained by the OLS and SAR models were relatively higher than those obtained for the aquatic reproductive modes (OLS: R^2 adj = 0.464, $F = 68.211$, $p = 0.00$; SAR: R^2 adj = 0.535, $F = 28.622$, $p < 0.001$). SAR models indicated only three significant correlations with the non-aquatic reproductive modes (TOPO, TSEASO, and EVERGREEN), whereas all variables in the OLS models were significant (Table 3).

In summary, irrespective of the reproductive specialization (aquatic or non-aquatic), we found major reproductive diversity along the Atlantic coast. This region is mostly characterized by the presence of ombrophilous forest, rugged topography, and humid climatic regimes with mild and less seasonality in temperatures. A lower number of reproductive modes was found in inland areas of the Atlantic Forest, mostly in the southeastern and southern Brazilian states. These areas are characterized by having semideciduous and deciduous forests, hot and more seasonal climate regimes, and less rugged topography than the coastal region. Despite the broadly similar diversity patterns of the aquatic and non-aquatic reproductive modes, the main difference between them is the steeper richness gradient in the non-aquatic reproductive modes. Among the selected environmental correlates, we found that the aquatic reproductive modes were better characterized by a general combination of climate, topography, and type of vegetation, whereas the non-aquatic reproductive modes were better described by specific variables related to climate stability (temperature seasonality), prevalence of humid microhabitats (quantity of evergreen forest), and rugged topography.

Discussion

Our initial predictions were supported by the results: (a) the aquatic reproductive modes were correlated with different aspects of climate (either general climatic trends or variables related to climatic seasonality), relief, and vegetation; and (b) the non-aquatic reproductive modes were specifically correlated with predictors related to lower oscillations in temperature on a yearly basis and the presence of evergreen forests in rugged topographic areas, thus emphasizing the necessity of humid forests and stable climate regimes for supporting higher levels of biological diversity (e.g., Müller *et al.* 2013, Vasconcelos *et al.* 2019) and, in the present study, different varieties of anuran reproductive modes with non-aquatic eggs.

Water is necessary for anurans because of their physiological needs (e.g., maintenance of a moist skin for effective cutaneous breathing) and reproductive characteristics (e.g., development of aquatic larvae or presence of humid microhabitats for development of eggs and juveniles with direct development; Duellman and Trueb 1994, Haddad *et al.* 2013). The necessity of water for anurans is reflected here

Table 1. Model selection of the Ordinary Least Square models for the reproductive modes with aquatic eggs. *N* = number of predictor variables in the respective model; AICc = Akaike Information Criterion corrected for small samples (sorted according to the lowest value); AICc WI = evidence support level for the respective model. See Materials and Methods for the abbreviations of variables.

Variables	***N***	**AICc**	**AICc WI**
AET+TOPO+TSEASO+PRECIP+DECIDUOUS+ EVERGREEN	6	153.653	0.39
AET+TOPO+TSEASO+PRECIP+PRECSEASO+ DECIDUOUS+EVERGREEN	7	154.679	0.233
AET+TOPO+TEMP+TSEASO+PRECIP+ DECIDUOUS+EVERGREEN	7	155.539	0.152
AET+TOPO+TEMP+TSEASO+PRECIP+ PRECSEASO+DECIDUOUS+EVERGREEN	8	156.119	0.114

Table 2. Model selection of the Ordinary Least Square models for the reproductive modes with non-aquatic eggs. *N* = number of predictor variables in the respective model; AICc = Akaike Information Criterion corrected for small samples (sorted according to the lowest value); AICc WI = evidence support level for the respective model. See Materials and Methods for the abbreviations of variables.

Variables	***N***	**AICc**	**AICc WI**
AET+TOPO+TEMP+TSEASO+PSEASO+ EVERGREEN	6	767.956	0.311
AET+TOPO+TEMP+TSEASO+PRECIP+ PRECSEASO+ EVERGREEN	7	769.076	0.178
AET+TOPO+TEMP+TSEASO+PRECSEASO+ DECIDUOUS+EVERGREEN	7	769.286	0.16
AET+TOPO+TEMP+TSEASO+PRECSEASO	5	769.919	0.117
AET+TOPO+TEMP+TSEASO+PRECIP+ PRECSEASO+ DECIDUOUS+EVERGREEN	8	770.289	0.097

Table 3. Results of the non-spatial Ordinary Least Squares (OLS) and spatially explicit Simultaneous Autoregressive models (SAR) (variable importance values ± standard error) to explain the variation in the number of reproductive modes of aquatic and non-aquatic eggs. Significant correlations ($p < 0.05$) are highlighted in bold.

Variables	**Aquatic eggs**		**Non-aquatic eggs**	
	OLS	SAR	OLS	SAR
INTERCEPT	**5.735 ± 0.413**	**2.46 ± 0.061**	**2.083 ± 0.025**	**1.602 ± 0.127**
AET	**0.097 ± 0.017**	**0.087 ± 0.016**	**0.114 ± 0.036**	0.045 ± 0.025
TOPO	**0.167 ± 0.016**	**0.111 ± 0.016**	**0.318 ± 0.032**	**0.137 ± 0.025**
TEMP	–	–	**-0.182 ± 0.045**	-0.047 ± 0.038
TSEASO	**-0.964 ± 0.123**	**-0.115 ± 0.026**	**-0.338 ± 0.044**	**-0.223 ± 0.052**
PRECIP	**0.049 ± 0.019**	0.02 ± 0.021	–	–
PSEASON	–	–	**0.172 ± 0.046**	-0.059 ± 0.046
DECIDUOUS	**-0.076 ± 0.019**	**-0.067 ± 0.017**	–	–
EVERGREEN	**0.077 ± 0.018**	**0.079 ± 0.016**	**0.066 ± 0.033**	**0.073 ± 0.024**

by the correlation of aquatic reproductive modes and water-related variables, such as AET and the presence of ombrophilous forests (i.e., evergreen forests). The amount of precipitation per se was only correlated with reproductive modes in the OLS model but not when the spatial autocorrelation was taken into account in the SAR model. This result indicates that the amount of precipitation per se is not always critical for supporting a high variability of aquatic reproductive modes, but an environmental water-energy balance that generates high primary productivity (i.e., places with high AET index) is also important, in addition to the presence of humid microhabitats that are constantly maintained within evergreen forests. Humid conditions may have been ideal for the evolution and establishment of species with aquatic reproductive modes in which the water accumulates in tree holes or in aerial plants, such as the Modes 6, 8, and 14 (sensu Haddad and Prado 2005). For non-aquatic reproductive modes, the SAR model indicated an implicit necessity of water for anurans because of the positive correlation with the presence of ombrophilous forests. The presence of water in the form of humid microhabitats generated by the heterogeneous structure of ombrophilous forests becomes a key opportunity for the development and establishment of reproductive specializations of non-aquatic eggs, such as direct development of terrestrial eggs deposited on the moist forest floor (Mode 23) or in arboreal structures (Mode 27) (Haddad and Prado 2005, Haddad *et al*. 2013).

Temperature oscillation throughout the year was a predictor for both aquatic and non-aquatic anuran reproductive modes. Regions having less temperature variation throughout the year supported more anuran reproductive modes. Greater variations in temperature values (especially for higher temperatures) may lead to lower values of humidity or to faster evaporation of water bodies. More stable temperatures may lead to breeding sites with enough humidity or volume of water throughout the year, which in turn should allow for the presence of a variety of reproductive modes in such regions. This result reinforces the idea that climatically stable regions support higher levels of biological diversity (e.g. Carnaval *et al*. 2009), as seen in the southeastern ombrophilous forests of the Atlantic Forest that support the highest diversity of reproductive modes. Warmer and more seasonally variable regions in inland areas of the Atlantic Forest support fewer types of reproductive modes but include the most common anuran reproductive mode (Mode 1: eggs and exotrophic tadpoles in lentic water; sensu Haddad and Prado 2005) and reproductive modes of wide-ranging species with aquatic (e.g., *Physalaemus cuvieri,* Mode 11) or non-aquatic (e.g., *Leptodactylus fuscus,* Mode 30) eggs associated with foam nests that typically avoid desiccation in these climatically harsher environments (Haddad and Prado 2005, Santos *et al*. 2009).

Topography was also identified as a correlate of anuran reproductive modes. Mountain uplifts favored diversification of different taxa and anuran reproductive modes (Haddad and Prado 2005, Rangel *et al*. 2018, Benício *et al*. 2021). This process was not the only source of selective pressures leading to the evolution of diverse reproductive modes (Haddad and Prado 2005). A region with high reproductive diversity depends on the presence of different aquatic/humid environments found within forests (Müller *et al*. 2013). When such a region is intersected by mountain chains, the major breeding habitats may be inaccessible to some populations, which in turn may have become more isolated. Evolution will favor those organisms that exploit the many small, humid microhabitats that become available to them. Prior to mountain uplifts, organisms of an ancestral species maintained gene flow among themselves, leading to common reproductive behaviors. The splitting of populations because of mountain uplifts, coupled with the constant presence of humid/aquatic microhabitats within evergreen forests, was an ideal scenario that favored new reproductive strategies, promoted genetic differentiation and speciation. In areas lacking ombrophilous forests or constant environmental humidity, higher rates of allopatric speciation in mountainous areas might still occur, but most species would probably exhibit generic reproductive modes with eggs and exotropic tadpoles in lentic (Mode 1) or lotic (Mode 2) environments or egg deposition in subterraneous foam nests (Modes 30 and 32 sensu Haddad and Prado 2005). The influence of topography on the evolution of anuran reproductive modes is corroborated by the high phylogenetic signal found for Atlantic Forest anurans. Benício *et al.* (2021) found that a higher speciation rate occurred when the coastal Atlantic Forest mountains emerged. Many of these coastal species, some of them from a particular genera or family (e.g., *Brachycephalus, Dendrophryniscus, Fritziana, Crossodactylodes,* Cycloramphidae) have unique reproductive modes associated with bromeliads, arboreal structures, or the forest floor, or have direct development, modes that are absent in inland regions where the climate is drier and the topography is not rugged.

The greater reproductive diversity found in coastal regions of the Atlantic Forest is broadly congruent with the taxonomic richness of anurans (Vasconcelos *et al*. 2010, 2014, 2019). Silva *et al*. (2012) found a positive correlation between the taxonomic richness and the number of reproductive modes in 27 anuran communities in the southeastern Atlantic Forest. These authors found that reproductive modes of these communities have a nested pattern of distribution and are correlated with high levels of environmental humidity. Localities with a low number of reproductive modes, mostly located in inland and drier regions, present the most generalized and widespread anuran reproductive modes. Silva *et al*. (2012) also found higher variability and unique types of reproduction in humid areas along the Atlantic Forest coast. Besides this nested pattern of distribution of reproductive modes in the Atlantic Forest, the absence of some anuran lineages with diversified reproductive modes in inland regions suggests that physiological or ecological tolerances have prevented coastal species and clades from occupying the inland region (i.e., the niche conservatism hypothesis; Wiens *et al.* 2010, Benício *et al.* 2021). Ecological traits that species and clades retain over their evolutionary history (i.e., a given set of combination of reproductive characteristics) play a strong role in shaping anuran communities and different reproductive modes across regions with different climatic regimes in the Atlantic Forest (Benício *et al.* 2021).

Our study identified predictors of reproductive modes of the diverse anuran fauna in the Atlantic Forest. Our results may be of interest to herpetologists and ecologists who monitor climate variation and the fragmentation of natural areas. Our data may help to identify threshold values for predictors that would be invaluable in establishing the conservation status of a given species (e.g., Rueda *et al.* 2015). In light of the current biodiversity crisis, dozens of Atlantic Forest anurans with diverse reproductive modes have been predicted to have no climatically suitable breeding areas by 2050 under various climate change scenarios (e.g., Vasconcelos *et al*. 2018). Future studies integrating the conservation biogeography under different climate change scenarios (e.g., Vasconcelos and Prado 2019) and the environmental integrity that supports high levels of anuran reproductive diversity might be promising approaches leading to an effective anuran conservation plan in the highly diverse Atlantic Forest.

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Appendix I. *Species list having aquatic reproductive modes and the respective reproductive mode number (sensu Haddad* et al. *2013). Mode 1: Eggs and exotrophic tadpoles in lentic water. Mode 2: Eggs and exotrophic tadpoles in lotic water. Mode 3: Eggs and early larval stages in constructed subaquatic chambers; exotrophic tadpoles in streams. Mode 4: Eggs and early larval stages in natural or constructed basins; subsequent to flooding, exotrophic tadpoles in ponds or streams. Mode 5: Eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds or streams. Mode 6: Eggs and exotrophic tadpoles in water in tree holes or aerial plants. Mode 8: Eggs and endotrophic tadpoles in water in tree holes or aerial plants. Mode 10: Bubble nest floating on pond; exotrophic tadpoles in ponds. Mode 11: Foam nest floating on pond; exotrophic tadpoles in ponds. Mode 13: Foam nest floating on water accumulated in constructed basins; exotrophic tadpoles in ponds. Mode 14: Foam nest floating on water accumulated on the axils of terrestrial bromeliads; exotrophic tadpoles in ponds. Mode 15: Eggs hatch into exotrophic tadpoles.*

Aparasphenodon arapapa (6), *A. brunoi (1), Aplastodiscus albofrenatus* (5), *A. albosignatus* (5), *A. arildae* (5), *A. cavicola* (5), *A. cochranae* (5), *A. ehrhardti* (5), *A. eugenioi* (5), *A. flumineus* (5), *A. ibirapitanga* (5), *A. leucopygius* (5), *A. perviridis* (5), *A. sibilatus* (5), *A. weygoldti* (5), *Arcovomer passarellii* (1), *Bokermannohyla astartea* (6), *B. capra* (2), *B. caramaschii* (2), *B. carvalhoi* (2), *B. circumdata* (1 and 2), *B. gouveai* (1 and 2), *B. hylax* (4), *B. luctuosa* (2 and 4), *B. martinsi* (2), *Ceratophrys aurita* (1), *Chiasmocleis alagoana* (1), *C. atlântica* (1), *C. capixaba* (1), *C. carvalhoi* (1), *C. leucostica* (10), *C. schubarti* (1), *Crossodactylodes bokermanni* (6), *Crossodactylus aeneus* (3), *C. caramaschii* (3), *C. dispar* (3), *C. gaudichaudii* (3), *C. grandis* (3), *C. schmidti* (3), *Dasypops schirchi* (1), *Dendrophryniscus berthalutzae* (8), *D. brevipollicatus* (8), *D. carvalhoi* (8), *D. krausae* (8), *Dendropsophus anceps* (1), *D. bipunctatus* (1), *D. branneri* (1), *D. elegans* (1), *D. giesleri* (1), *D. meridianus* (1), *D. microps* (1), *D. minutus* (1), *D. nahdereri* (1), *D. nanus* (1), *D. novaisi* (1), *D. oliveirai* (1), *D. pseudomeridianus* (1), *D. sanborni* (1), *D. seniculus* (1), *D. soaresi* (1), *D. studerae* (1), *Elachistocleis cesarii* (1), *E. erythrogaster* (1), *Frostius pernambucensis* (8), *Hylodes asper* (3), *H. babax* (3), *H. cardosoi* (3), *H. charadranaetes* (3), *H. lateristrigatus* (3), *H. nasus* (1), *H. ornatus* (3), *H. otavioi* (3), *H. perere* (3), *H. perplicatus* (3), *H. phyllodes* (3), *H. regius* (3), *H. sazimai* (3), *Hyophryne histrio* (1), *Hypsiboas albomarginata* (1), *H. albopunctata* (1), *H. atlanticus* (1 and 2), *H. bischoffi* (1), *H. caingua* (1), *H. caipora* (2), *H. crepitans* (4), *H. curupi* (2), *H. exastis* (4), *H. faber* (1 and 4), *H. guentheri* (1), *H. joaquini* (2), *H. latistriatus* (2), *H. leptolineatus* (1 and 2), *H. marginatus* (2), *H. pardalis* (4), *H. polytaenius* (1), *H. pombali* (1 and 2), *H. prasinus* (1 and 2), *H. pulchellus* (1), *H. punctatus* (1 and 2), *H. raniceps* (1), *H. semiguttatus* (1 and 2), *H. semilineatus* (1 and 2), *H. stellae* (1 and 2), *Itapotihyla langsdorffii* (1), *Leptodactylus flavopictus* (13), *L. labyrinthicus* (11), *L. latrans* (11), *L. natalensis* (13), *L. podicipinus* (13), *L. vastus* (11), *L. viridis* (11), *Limnomedusa macroglossa* (1), *Lithobates palmipes* (1), *Macrogenioglottus alipioi* (1), *Melanophryniscus vilavelhensis* (6), *M. admirabilis* (1), *M. cambaraensis* (1), *M. dorsalis* (1), *M. moreirae* (1), *M. simplex* (2), *M. tumifrons* (1), *Odontophrynus americanus* (1), *O. carvalhoi* (2), *O. maisuma* (1), *Paratelmatobius cardosoi* (1), *P. gaigeae* (1), *Phyllodytes acuminatus* (6), *P. edelmoi* (6), *P. gyrinaethes* (6), *P. kautskyi* (6), *P. luteolus* (6), *P. melanomystax* (6), *P. tuberculosus* (6), *P. wuchereri* (6), *Physalaemus aguirrei* (11), *P. atlanticus* (11), *P. crombiei* (11), *P. cuvieri* (11), *P. erikae* (11), *P. feioi* (11), *P. jordanensis* (11), *P. kroyeri* (11), *P. lateristriga* (11), *P. lisei* (11), *P. maculiventris* (11), *P. maximus* (11), *P. moreirae* (11), *P. nanus* (11), *P. obtecus* (11), *P. olfersii* (11), *P. signifer* (11), *P. spiniger* (11 and 14), *Pipa carvalhoi* (15), *Proceratophrys appendiculata* (1 and 2), *P. avelinoi* (2), *P. bigibbosa* (2), *P. boiei* (1 and 2), *P. brauni* (2), *P. cristiceps* (2), *P. laticeps* (1 and 2), *P. melanopogon* (1 and 2), *P. renalis* (2), *P. sanctaritae* (2), *P. schirchi* (2), *P. subguttata* (2), *Pseudis bolbodactyla* (1), *P. cardosoi* (1), *P. fusca* (1), *P. minuta* (1), *Pseudopaludicola falcipes* (1), *Rhinella abei* (1 and 2), *R. achavali* (1), *R. crucifer* (1 and 2), *R. dorbignyi* (1), *R. fernandezae* (1), *R. granulosa* (1), *R. henseli* (1 and 2), *R. hoogmoedi* (1), *R. icterica* (1 and 2), *R. jimi* (1), *R. ornata* (1 and 2), *R. pygmaea* (1), *R. schneideri* (1 and 2), *Scinax agilis* (1), *S. albicans* (2), *S. alter* (2), *S. angrensis* (1), *S. argyreornata* (1, *S. ariadne* (2), *S. aromothyella* (1), *S. auratus* (1), *S. belloni* (2), *S. brieni* (2), *S. caldarum* (1), *S. carnevallii* (1), *S. catharinae* (2), *S. crospedospilus* (1), *S. cuspidatus* (1), *S. duartei* (1), *S. eurydice* (1), *S. flavoguttatus* (2), *S. fuscomarginatus* (2), *S. fuscovarius* (1), *S. granulatus* (1), *S. hayii* (1), *S. heyeri* (2), *S. hiemalis* (1), *S. humilis* (1), *S. imbegue* (1), *S. insperatus* (6), *S. juncae* (1), *S. littoralis* (1), *S. littoreus* (6), *S. longilineus* (2), *S. luizotavioi* (1 and 2), *S. machadoi* (2), *S. obtriangulatus* (2), *S. pachycrus* (1), *S. perereca* (1), *S. perpusillus* (6), *S. ranki* (1), *S. rizibilis* (1), *S. similis* (1), *S. squalirostris* (1), *S. strigilatus* (1 and 2), *S. trapicheiroi* (1), *S. tymbamirim* (1), *S. uruguayus* (1), *S. v-signatus* (1), *S. x-signatus* (1), *Scythrophrys sawayae* (1), *Sphaenorhynchus botocudo* (1), *S. caramaschii* (1), *S. palustris* (1), *S. planicola* (1), *S. prasinus* (1), *S. surdus* (1), *Stereocyclops incrassatus* (1), *S. parkeri* (1), *Trachycephalus typhonius* (1), *T. atlas* (1), *T. dibernardoi* (1), *T. imitatrix* (1), *T. lepidus* (1), *T. mesophaeus* (1)*, T. nigromaculatus* (1 and 2), *Xenohyla truncate* (1).

Appendix II. *Species list having non-aquatic reproductive modes and the respective reproductive mode number (sensu Haddad* et al. *2013). Mode 18: Eggs on ground or rock above water; upon hatching, exotrophic tadpoles move to water. Mode 19: Eggs on humid rocks, in rock crevices, or on tree roots above water; exotrophic semiterrestrial tadpoles living on rocks and rock crevices in a water film or in the water–land interface. Mode 20: Eggs hatching into exotrophic tadpoles that are carried to water by adult. Mode 21: Eggs hatching into endotrophic tadpoles that complete their development in the nest. Mode 23: Direct development of terrestrial eggs. Mode 24: Eggs hatching into exotrophic tadpoles that drop in lentic water. Mode 25: Eggs hatching into exotrophic tadpoles that drop in lotic water. Mode 27: Eggs hatching into froglets. Mode 30: Foam nest with eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds. Mode 32: Foam nest in subterranean constructed chambers; endotrophic tadpoles complete development in nest. Mode 36: Eggs carried on dorsum or in dorsal pouch of female; endotrophic tadpoles in bromeliads or bamboo. Mode 37: Eggs carried on dorsum or in dorsal pouch of female; direct development into froglets.*

Adelophryne pachydactyla (23), *Adenomera ajurauna* (32), *A. araucaria* (32), *A. bokermanni,* (32), *A. marmorata* (32), *A. nana* (32), *A. thomei* (32), *Agalychnis aspera* (18), *A. granulosa* (25), *Allobates olfersioides* (20), *Brachycephalus alipioi* (23), *B. didactylus* (23), *B. ephippium* (23), *B. ferruginus* (23), *B. guarani* (23), *B. hermogenesi* (23), *B. margaritatus* (23), *B. nodoterga* (23), *B. pulex* (23), *B. toby* (23), *B. tridactylus* (23), *B. vertebralis* (23), *Cycloramphus lutzorum* (19), *C. acangatan* (21), *C. boraceiensis* (19), *C. brasiliensis* (19), *C. dubius* (19), *C. eleutherodactylus* (21), *C. izecksohni* (19), *C. juimirim* (19), *C. rhyokonastes* (19), *C. valae* (19), *Dendropsophus berthalutzae* (24), *D. decipiens* (24), *D. haddadi* (24), *Euparkerella brasiliensis* (23), *E. cochranae* (23), *E. robusta* (23), *Fritziana fissilis* (36), *F. goeldii* (36), *F. ohausi* (36), *Gastrotheca albolineata* (37), *G. ernestoi* (37), *G. fissipes* (37), *G. fulvorufa* (37), *G. megacephala* (37), *G. microdiscus* (37), *G. prasina* (37), *G. pulchra* (37), *G. recava* (37), *Haddadus binotatus* (23), *Holoaden bradei* (23), *H. luederwaldti* (23), *Ischnocnema bolbodactyla* (23), *I. concolor* (23), *I. guentheri* (23), *I. henselii* (23), *I. hoehnei* (23), *I. juipoca* (23), *I. manezinho* (23), *I. nasuta* (27), *I. parva* (23), *I. sambaqui* (23), *I. verrucosa* (23), *I. vizottoi* (23), *Leptodactylus cupreus* (30), *L. furnarius* (30), *L. fuscus* (30), *L. gracilis* (30), *L. jolyi* (30), *L. mystaceus* (30), *L. mystacinus* (30), *L. notoaktites* (30), *L. plaumanni* (30), *L. spixi* (30), *L. troglodytes* (30), *Myersiella microps* (23), *Paratelmatobius poecilogaster* (18), *Phasmahyla spectabilis* (25), *P. cochranae* (25), *P. exilis* (25), *P. guttata* (25), *P. jandaia* (25), *Phrynomedusa marginata* (18), *Phyllomedusa bahiana* (24), *P. burmeisteri* (24), *P. distincta* (24), *P. iheringii* (24), *P. nordestina* (24), *P. rohdei* (24), *P. tetraploidea* (24), *Pristimantis paulodutrai* (23), *P. ramagii* (23), *P. vinhai* (23), *Sphaenorhynchus pauloalvini* (24), *Thoropa lutzi* (19), *T. miliaris* (19), *T. saxatilis* (19), *Vitreorana eurygnatha* (25), *V. uranoscopa* (25), *Zachaenus parvalus* (21).