Oecologia Australis
28(2):112–128, 2024
http://doi.org/10.4257/oeco.2024.2802.03

ECOLOGICAL NICHE MODELING OF TWO SEMI-AQUATIC SNAKES (SERPENTES: DIPSADIDAE) FROM THE BRAZILIAN ATLANTIC FOREST

André Felipe Barreto-Lima[1]*, *Renato Silveira Bérnils*[2]
& Rodrigo Castellari Gonzalez[3]

[1] Instituto Nacional da Mata Atlântica, Av. José Ruschi, 4, Centro, CEP 29650-000, Santa Teresa, ES, Brazil.

[2] Universidade Federal do Espírito Santo, Centro Universitário Norte do Espírito Santo, Departamento de Ciências Agrárias e Biológicas, Rodovia Governador Mário Covas, Km 60, Litorâneo, CEP 29932-540, São Mateus, ES, Brazil.

[3] Universidade Estadual do Ceará, Museu de História Natural do Ceará Prof. Dias da Rocha, Rua Divino Salvador, 225, Centro, CEP 62770-000, Pacoti, CE, Brazil.

E-mails: afblima1@gmail.com (*corresponding author); renatobernils@gmail.com; rodcastgon@gmail.com

---

Abstract: We approached spatial ecology with ecological considerations for conservation of two snake species with resembling distributions along fragmented landscapes of the Brazilian Atlantic Forest, *Gomesophis brasiliensis* and *Ptychophis flavovirgatus*. Both are Neotropical snakes with allopatric groups, showing intriguing geographic distribution patterns with large gap areas amongst them. We aimed to predict the distribution pattern of both species and determine if their ecological niches overlap. To test the hypothesis of niche overlapping, in the Niche equivalency test (Net) and Similarity test (Bst), we evaluated the niche models for both species based on the georeferenced environmental layers (bioclimatic, geographic, and vegetation), and using the software Maxent v.3.3.3. The potential distribution of both species was similar with large sympatric areas, both in grassy landscapes of the Atlantic Forest, although *G. brasiliensis* is evenly distributed in southeastern and southern Brazil, while *P. flavovirgatus* is more concentrated in southern Brazil. Altitude and minimum temperature of the coldest month were the most important variables for both species in their distribution models. Similar and equivalent niches overlapping between species indicated a conservative niche for both species. The niches' overlap may be explained by environmental influences along with phylogenetic inertia.

Keywords: *Gomesophis*, Niche overlap, *Ptychophis*, Species distribution modelling

---

INTRODUCTION

Biogeographic studies have made important advances in the understanding of large-scale ecological patterns on natural populations (Hawkins 2004), to know their distribution, ecology, and actions for conservation. In times of global environmental changes, identifying the factors that shape species' ecological niches and understanding how they operate can help to draft more effective conservation plans. By changing climatic conditions and, consequently, the ecological factors that favor the occurrence of species, it is possible to alter, restrict, or even eliminate the permanence of species throughout their natural distributions. In addition, the differences in the ecological factors that shape species distributions may help to highlight different niches between closely related taxa (see Aguirre-Gutierrez *et al.* 2015). On the other hand, the conservatism of ecological niches has become a concern given the expected impacts of climate change on biodiversity (see Thomas *et al.* 2004, Chen *et al.* 2011, Araujo *et al.* 2013, Aguirre-Gutierrez *et al.* 2015). The knowledge about biodiversity remains insufficient because a large part of global biodiversity is yet to be formally described (Linnean shortfall), and because geographical distributions of most species are yet gapped and poorly understood (Wallacean shortfall) (Lomolino 2004, Whittaker *et al.* 2005, Bini *et al.* 2006). Thereby, the existence of these shortfalls makes it hard to document and interpret biological data (Bini *et al.* 2006, Oliveira *et al.* 2016, Nogueira *et al.* 2019), particularly for snakes, because despite the large efforts to understand and map their distributions (see Nogueira *et al.* 2019), the available data is still insufficient for many species, especially in the Neotropics (Oliveira-Dalland *et al.* 2022).

One in every five species of reptiles is endangered, most of them in tropical forested areas (Cox *et al.* 2022), especially due to habitat loss (Gibbons *et al.* 2000, Driscoll 2004, ICMBio 2018, IUCN 2022). Some of the main threats to reptile conservation are very well-known: destruction and habitat loss (forests and water bodies), illegal hunting, construction of hydroelectric dams, urbanization, pollution, and mining; and these threats alone or combined are severely harmful to the herpetofauna (see Barreto-Lima & Simoncini 2019 and its references). Yet, climate change and global warming as a consequence of direct or indirect human activities (such as the use of fossil fuel, agricultural and livestock cultures, and forest fires) have extirpated much of the world's biodiversity, mainly in the Neotropics (Barreto-Lima & Simoncini 2019). Therefore, studying biodiversity is urgent since it is globally disappearing at a large pace. In this scenario, great attention has been paid to the use of Species Distribution Modeling (SDM), which relates species occurrence records with environmental predictors to identify suitable areas for potential occurrence (Franklin 2010). Considering the Environmental Niche Models (ENM), a pair of species may have niche similarity, when the niches may be used to predict one another's known occurrences, usually as a consequence of phylogenetic relationships and/or niche equivalency if such niches are indistinguishable (Warren *et al.* 2008). Therefore, SDM and ENM are tools that help understanding the species distribution and their overlapping niches in a given area (Warren *et al.* 2008, Zank *et al.* 2014, Costa *et al.* 2015).

Figure 1. Live specimen of *Gomesophis brasiliensis* (IBSP 88759) from the Parque Estadual da Serra do Papagaio, Minas Gerais, Brazil (Photo: F. de A. Menezes).

Tachymenini is a monophyletic tribe of Xenodontinae (Pyron *et al.* 2013, Trevine *et al.* 2022), which comprises 36 small, opisthoglyphous, and viviparous species of South America (Wallach *et al.* 2014, Nogueira *et al.* 2019). The species of this tribe are strictly terrestrial, except *Gomesophis brasiliensis* (Figure 1) and *Ptychophis flavovirgatus* (Figure 2) which are the only ones that use aquatic environments (Lema & Deiques 1992, Marques *et al.* 2001, 2004, Lema 2002, Gonzalez *et al.* 2014, Menezes *et al.* 2018). They occur in the Atlantic Forest of southern and southeastern Brazil, with a few records of *G. brasiliensis* in central Brazil (Gonzalez *et al.* 2014, Nogueira *et al.* 2019). Populations are sympatric in several locations, commonly in elevated areas of the subtropical climate, in grassy fields of the 'Araucaria' Forest (Porto & Caramaschi 1988, Marques *et al.* 2001, 2004, Lema 2002, Gonzalez *et al.* 2014, Nogueira *et al.* 2019), nevertheless, both species present intriguing distribution patterns, with large gap areas amongst populations (Gonzalez *et al.* 2014, Nogueira *et al.* 2019).

Since they are sister species (see Trevine *et al.* 2022), despite the differences in their distribution patterns, we hypothesized the existence of conservatism niches with similar ecologies between them (*i.e.*, used environmental niches are conserved over evolutionary time), because closely related species are expected to have similar, but rarely identical, environmental niches (Warren *et al.* 2008). Thereby, we tested two alternative hypotheses by Peterson *et al.* (1999) and Graham *et al.* (2004) for the role of niche conservatism in speciation: (1) the hypothesis of niche equivalency, rejected by Graham *et al.* (2004), which predicts no significant differences between alternative niche models, and (2) the hypothesis of niche similarity, supported by Peterson *et al.* (1999), which predicts niches can be more similar than expected by chance under a specific null model (Warren *et al.* 2008). In addition, we assessed the potential distribution patterns of *P. flavovirgatus* and *G. brasiliensis* to understand the ecological reasons that determine the gaps in their geographic distributions and to find out if their ecological niches overlap. Finally, we draw attention to the importance of these areas for the conservation of these species.

Figure 2. Live specimen of *Ptychophis flavovirgatus* (MCP 10979) from Guarapuava, Paraná, Brazil (Photo: A. Kwet).

MATERIAL AND METHODS

Data collection

We examined specimens and collected data from nine herpetological collections (Appendix I) and confirmed the geographic coordinates of each record by using Google Earth v.7.3 (Lisle 2006). When no specific locality was found, we used the geographic coordinates of the municipality centroid (IBGE 2023). Imprecise, dubious, and duplicate sites were discarded, therefore we used 79 records (47 of *G. brasiliensis*, and 32 of *P. flavovirgatus*) to generate both the potential distribution maps (SDM) and the niche overlap analysis (ENM) between them. The distribution maps were generated in Quantum Gis v.QGIS 3.30.2 (Menke *et al.* 2016).

Species distribution modeling – SDM

We obtained data on the topographic aspect (m), bioclimatic variables (Bio1 to Bio19) for the last 50 years (WorldClim databank: Global Climate Data: http://www.worldclim.org/version1), and the normalized difference vegetation index-NDVI (vegetal cover) from NASA (Huete *et al.* 2002). First, repeated records (from the same sampling points) were removed from the analyzes to avoid biases in the modeling results. To avoid spatial autocorrelation among the data, we excluded the highly correlated variables ($r > 0.75$; $p < 0.005$), using correlation tests among the environmental variables to avoid overlapping or redundancies and collinearity in the models (> 75% were discarded). After the first model analysis, we discarded variables of the probability scores (%) that were zero or very close to zero (*e.g.*, 0.1), and ran a new model with the remaining variables. We performed multiple regressions relating environmental variables and coordinates of each location (Bocard *et al.* 1992). This analysis was complemented by the selection of the environmental variables based on the Akaike information criterion and "model averaging method" (Burnham & Anderson 2002). We used the R statistical software v.2.15 ($p < 0.05$) in all tests. This way, we used only eight variables for the SDM of each occurrence record, in a spatial resolution of 2.5 arc-minutes (~5 km grid cell size at the equator): altitude (m), NDVI, vegetal cover (intensity scale: from 0 to 255), mean diurnal temperature range (Bio2), minimum temperature of the coldest month (Bio6), temperature annual range (Bio7), mean temperature of the wettest quarter (Bio8), annual mean precipitation (Bio12), and precipitation in the warmest month (Bio18).

We created the distribution models (SDM) in Maxent v.3.3.3 based on the average test of the AUC (area under the curve) for the replicate runs (Phillips *et al.* 2006), standard deviation (SD), omission error, and binomial probability. This software uses only the presence (occurrence data) and environmental parameters to estimate suitable areas for the potential occurrence of species, by minimizing the relative entropy between two probability densities, defined in the covariate space: one estimated from the presence data and another from the landscape (Elith *et al.* 2011). Ten distribution models were generated for each species, considering the average of fold cross-validation for the creation of a final model, using a random selection of the points of occurrences recorded for training (70%) and for tests (30%) performed.

Additionally, we validated the final model with a regularization multiplier by comparing with indices (AUC and 10% Omission Rate) of other models obtained, according to the regularization multipliers used (*i.e.*, 0.5, 1.0, 1.5, and 2.0, Miranda *et al.* 2015). Since all AUC values were higher than 0.9 (90%), we chose models with the greatest value of AUC (and the lowest values of SD), and the lowest values referring to the logistic threshold of the 10% training presence for the use of the parameters in subsequent modeling steps. This last parameter refers to the likelihood of finding favorable conditions for each species to occur when using the lowest value attributed to any of the 90% of occurrence records with the highest scores (Miranda *et al.* 2015).

We also used the default configuration of Maxent (with the algorithm generating AUC response curves) and the Jackknife statistical test to estimate the importance of each variable contribution to the model of potential distribution (*i.e.*, the relative percentage contribution and the permutation of variables). Then, estimates of relative contributions of the environmental variables to the Maxent (v.3.3.3k) model were generated: percent contribution (PC) and permutation importance (PI), both normalized to percentages. To determine the PC, in each iteration of the training algorithm, we added the increase in regularized gain to the contribution of the corresponding variable or subtracted it if the change to the absolute value of lambda was negative. To determine the PI for each environmental variable, in turn, the values of that variable on training presence and background data were randomly permuted.

Overlap of ecological niche models – ENM

In order to test the hypothesis of ecological niche overlap between a pair of species, with equivalence and similarity tests (Niche identity test = Net; and Background similarity test = Bst), we created environmental niche models (ENM) for both species with georeferenced layers of the same environmental variables from the WorldClim and NDVI. We used Maxent (v.3.3.3), within the R (v.2.15), and the packages 'dismo', 'maptools', and 'phyloclim' (v.0.9-3) to generate the Net and Bst indexes.

Background similarity test (Bst) and Niche identity test (Net)

We considered the Background similarity test (Bst) and Niche identity test (Net), which are measures of similarity (D and I values), initially based on Hellinger's distance (van der Vaart 1998), resulting from each species' niche, to compare the distribution of observed and expected frequencies (Warren *et al.* 2008). Both Net and Bst range from '0–1'; with 0 meaning absence and 1 being the maximum overlap between two species. These descriptive metrics can be used to test the two alternative hypotheses addressed by Peterson *et al.* (1999) and Graham *et al.* (2004) for the role of niche conservatism in speciation.

Graham *et al.*'s test (2004) – *i.e.*, the test of Niche equivalency (Net) – estimates if niches of closely-related species are effectively identical. The observed values of I and D are compared to the percentiles of the null distributions in a one-tailed test to evaluate the hypothesis that niche models for species X and Y are not significantly different, in other words, if they are equivalent (see Warren *et al.* 2008). Thus, the statistical null hypothesis predicts if closely-related species have different niches more than expected by chance. We randomly selected models 99 times to measure the distance in the environmental space of I and D values.

Conservative niches are based on Peterson *et al.*'s (1999) test – test of Niche similarity (Bst), which assesses whether the binomial distribution models from species predict each other's known occurrences, under the expectation from the null hypothesis that provides no information about each other's range (Warren *et al.* 2008): the species do not have similar niches, because the distributions are very different from each other. Thereby, Bst is treated as a two-tailed test because results outside of the null distribution in either direction are both biological and plausible (Warren *et al.* 2008) being the niches more (or perhaps less) similar between the species. We ran this analysis 99 times in both directions to construct the expected distributions of I and D values. Tests that generated the chi-square of Peterson *et al.* (1999) were randomized and applied to the ecological niche models (Warren *et al.* 2008). We considered $p \leq 0.05$ in all tests to reject the null hypothesis.

RESULTS

Geographic distribution patterns

Gomesophis brasiliensis occurred in the 'Cerrado' biome, in the Federal District (DF), but it was predominantly found in the Atlantic Forest, in the Brazilian states of Minas Gerais (MG), São Paulo (SP), Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS), between 16º to 31ºS and 44º to 54ºW (Figure 3). Most of the records were in elevations from 423 – 1,332 m (mean 873 m above the sea level, hereafter a.s.l), although it was also found at lower elevations, down to sea level, in RS, its southernmost records. Its distribution may be arranged into three areas (Figure 3, black circles): one small, isolated in DF, and two larger; one in MG and SP (Southern-MG+SP) and another farther south (PR+SC+RS). There are two important gaps among these groups: a larger gap between DF and southwestern MG, and a smaller gap in the southern half of SP as far as PR.

Ptychophis flavovirgatus was found exclusively in the Atlantic Forest, in MG, PR, SC, and RS, between 21° to 29°S and 44° to 54°W (Figure 4), from 0 – 1.058 m (mean 863 m a.s.l.). Most records were from higher elevations, although one specimen was found at sea level in the municipality of Porto Alegre (RS), where the greatest variation in elevation was found. The distribution of *P. flavovirgatus* falls into three areas (Figure 4, black circles): one in southern MG (Southern-MG), another in PR and northern SC (PR+Northern-SC), and the last one in southern SC and RS (Southern-SC+RS); with two remarkable gaps: one corresponding to the entire state of SP, and a smaller one in central SC.

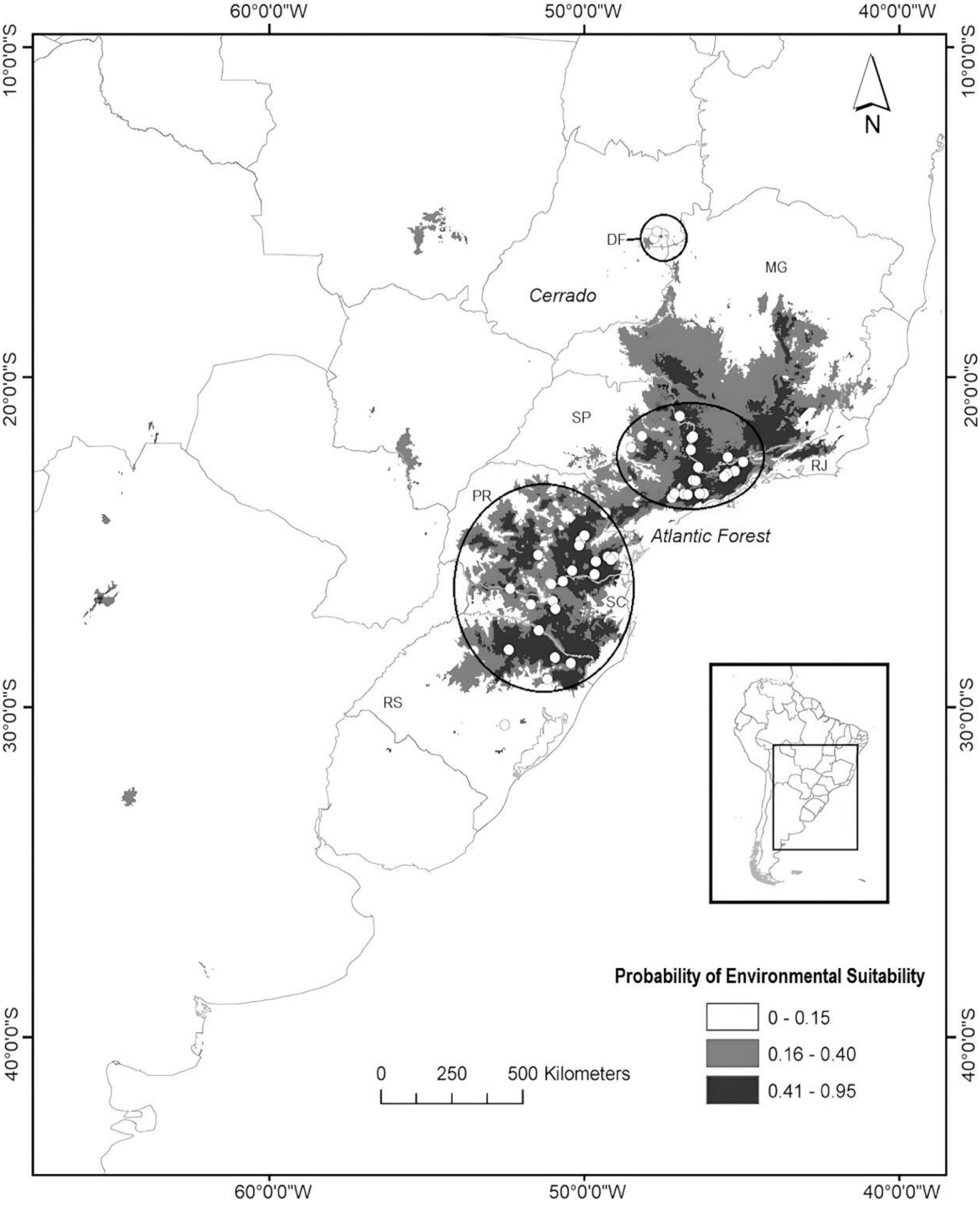

Figure 3. Environmental suitability for *Gomesophis brasiliensis* (%) showing three areas of population concentrations. Model from Maxent v. 3.3.3 (mean AUC = 0.986, SD = 0.006). White dots are sites of currently known occurrences. Brazilian states: Central-West: DF = Distrito Federal; Southeast: MG = Minas Gerais, RJ = Rio de Janeiro, SP = São Paulo; South: PR = Paraná, RS = Rio Grande do Sul, SC = Santa Catarina.

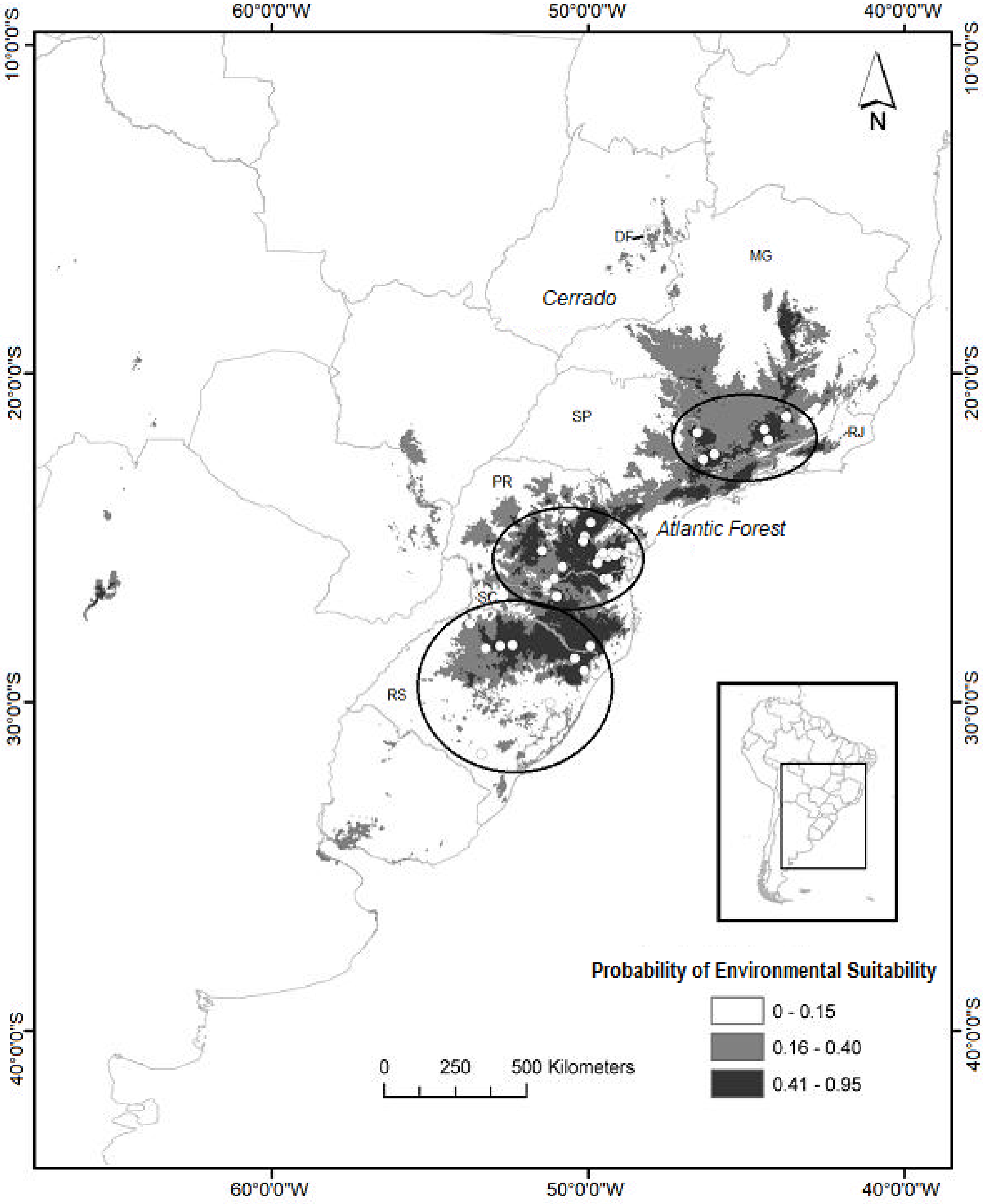

Figure 4. Environmental suitability for *Ptychophis flavovirgatus* (%) showing three areas of population concentrations in Brazil. Model from Maxent v. 3.3.3 (AUC = 0.985, SD = 0.016). White dots are sites of currently known occurrences. Brazilian states: Central-West: DF = Distrito Federal; Southeast: MG = Minas Gerais, RJ = Rio de Janeiro, SP = São Paulo; South: PR = Paraná, RS = Rio Grande do Sul, SC = Santa Catarina.

Species distribution modeling (SDM)

The areas with the highest probability of environmental suitability for *G. brasiliensis* were concentrated into two nuclear regions: MG+SP and PR+SC+RS (Figure 3, black and gray areas). The distribution area based on the model included both low and high elevations (average test AUC for the replicate runs = 0.987; SD = 0.006). For *P. flavovirgatus*, the highest probability of environmental suitability (%) was concentrated into three large nuclear areas: MG, PR+SC, and SC+RS (Figure 4, black and gray areas). The distribution area based on the model included numerous elevated areas in the mountains of the South Brazilian Plateau, where the temperatures are colder (the average test AUC for the replicate runs = 0.985; SD = 0.016). Altitude (Alt) and Bio 6 - minimum temperature of the coldest month were the most important environmental variables for both species in the SDMs, but specifically, Bio 18 - precipitation in the warmest month (for *G. brasiliensis*) and Bio 2 - mean diurnal temperature range (*P. flavovirgatus*) were the third most important environmental variables in the SDMs (Tables 1-2).

Overlap of environmental niche models (ENMs)

According to the Net results between *G. brasiliensis* and *P. flavovirgatus*, both indices (D and I) confirmed the niche equivalency (Net) to be more than the expected by chance: D = 0.732, p = 0.28442; I = 0.928, p = 0.37181, with p-value based on 100 permutations (Figure 5). The results of Bst for both indexes and directions also indicated more similarity of niches between the species than expected by chance (Table 3), considering the confidence intervals on 100 permutations (Figure 6).

Table 1. Most important environmental variables in the distribution models of *Gomesophis brasiliensis* (N = 47 sites). Alt = altitude, Bio 6 = minimum temperature of the coldest month, Bio 18 = precipitation in the warmest month, Bio 2 = monthly means (maximum temperature – minimum temperature), Bio 12 = annual mean precipitation, Bio 7 = annual temperature range, NDVI= normalized difference vegetation index (vegetal cover), and Bio 8 = mean temperature of the wettest quarter.

Variables	**Percent contribution (%)**	**Permutation importance (%)**
Alt	36.5	34.9
Bio 6	22.6	18.9
Bio 18	14.7	1.7
Bio 2	10.1	22.1
Bio 12	7.7	9.2
Bio 7	5.2	7.5
NDVI	3.1	5.5
Bio 8	0.1	0

Table 2. Most important environmental variables in the distribution models of *Ptychophis flavovirgatus* (N = 32 sites). Alt = altitude, Bio 6 = minimum temperature of the coldest month, Bio 2 = monthly means (maximum temperature – minimum temperature), Bio 18 = precipitation in the warmest month, Bio 7 = temperature annual range, Bio 12 = annual mean precipitation, NDVI= normalized difference vegetation index (vegetal cover), and Bio 8 = mean temperature of the wettest quarter.

Variables	**Percent contribution (%)**	**Permutation importance (%)**
Alt	24.6	18.1
Bio 6	24.1	14.2
Bio 2	22.3	23.4
Bio 18	11.7	0.4
Bio 7	8.3	33.2
Bio 12	6.6	7.7
NDVI	2.2	3.1
Bio 8	0.3	0

Table 3. Background similarity test (Bst) between *Gomesophis brasiliensis* and *Ptychophis flavovirgatus* with confidence intervals based on 100 permutations (95% confidence intervals; x versus random y, and y versus random x).

Index of niche overlap	**95% confidence intervals**	
	G. brasiliensis vs. random *P. flavovirgatus*	*P. flavovirgatus* vs. random *G. brasiliensis*
D = 0.746	(0.108, 0.157)	(0.122, 0.167)
I = 0.932	(0.294, 0.385)	(0.312, 0.394)

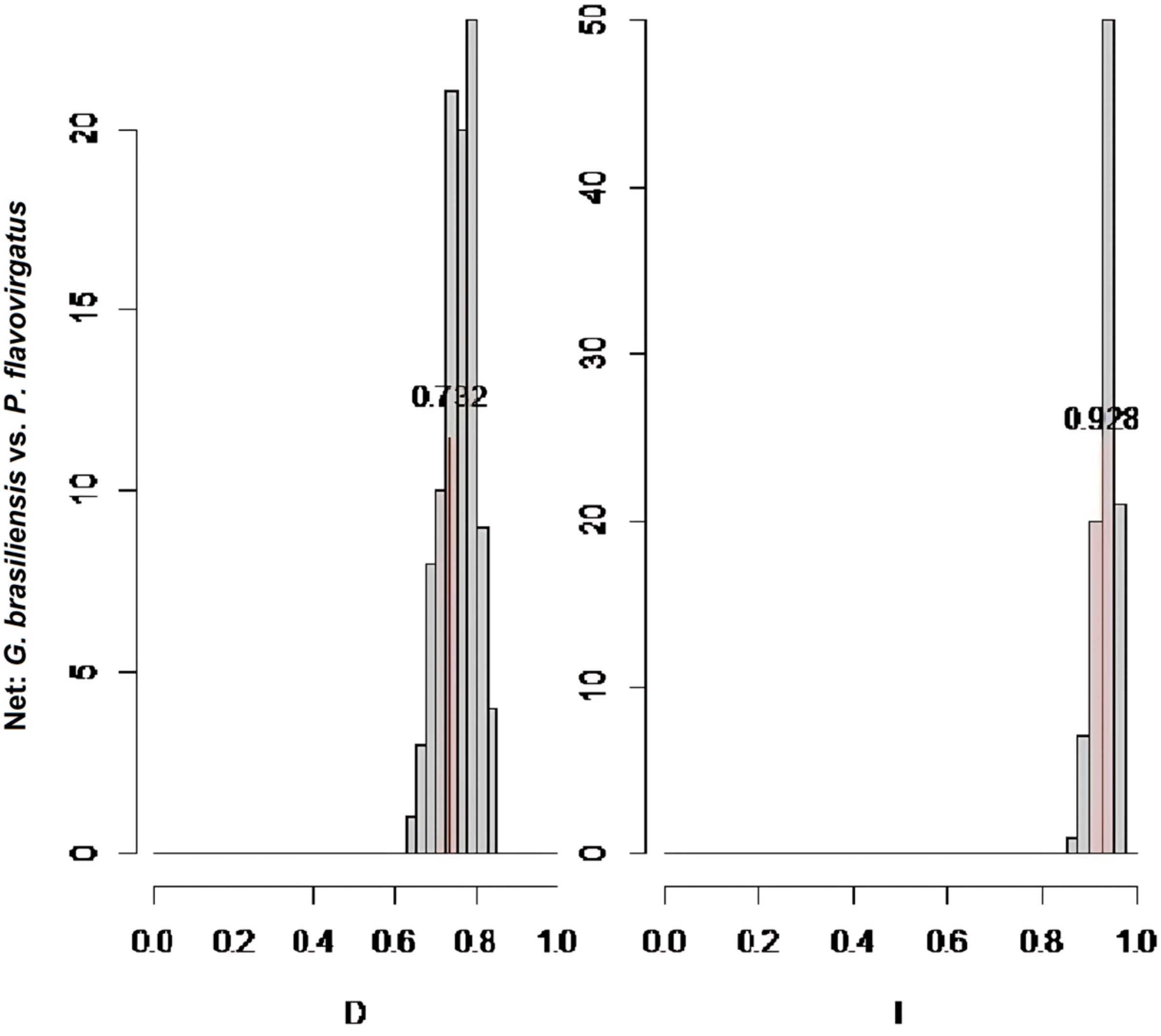

Figure 5. Niche equivalency Test (Net) on the overlap index D of Schoener (1968) and the similarity index I of Warren et al. (2008), based on 100 permutations between the species *Gomesophis brasiliensis* and *Ptychophis flavovirgatus* (total N = 79 records), showing niches equivalence for more than the expected by chance (p > 0.05) (null distributions represented by gray bars).

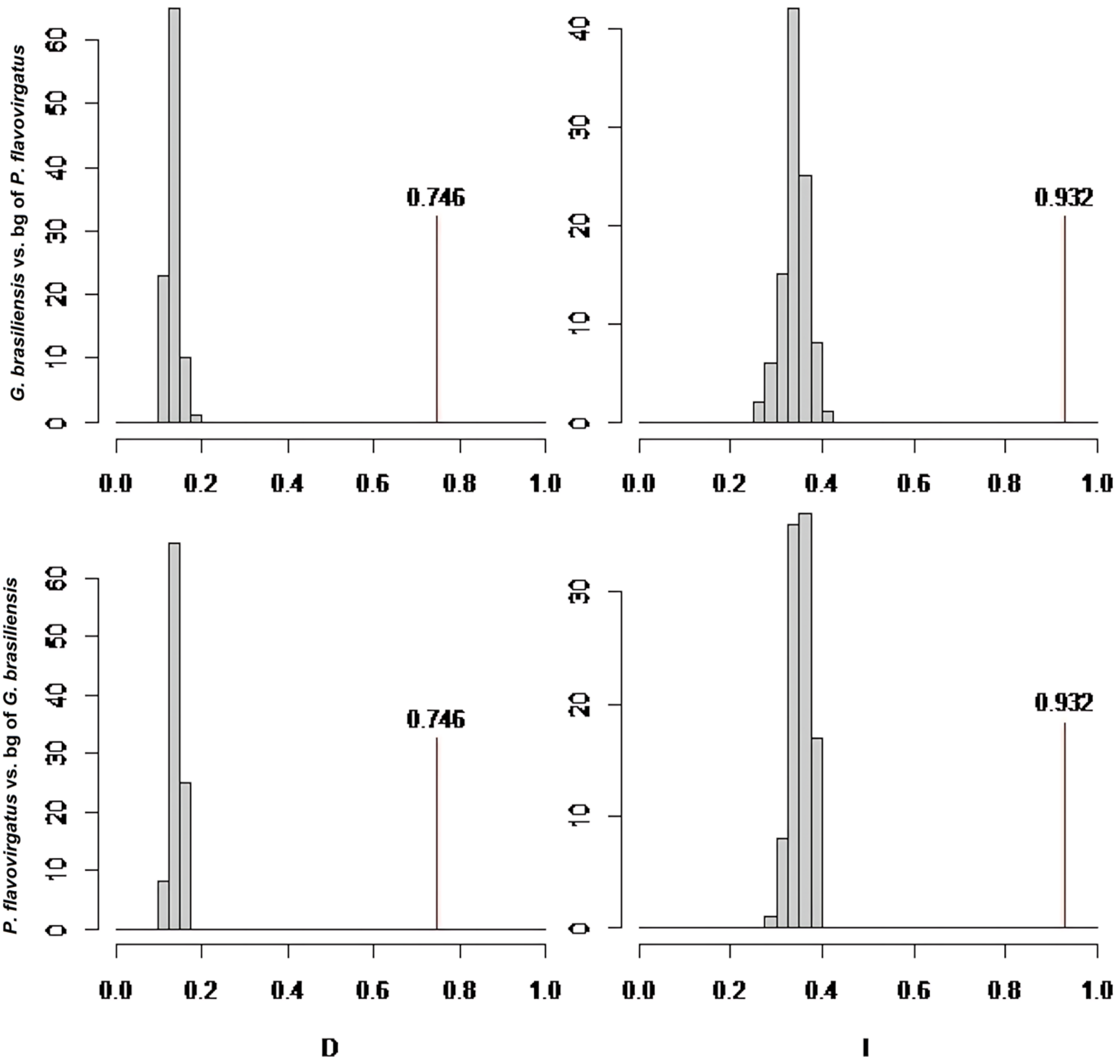

Figure 6. Test of niche similarity (Bst) on the overlap index and the similarity index, between *Gomesophis brasiliensis* and *Ptychophis flavovirgatus* (N = 79 records), indicating more niche similarity than the expected by chance, based on 100 permutations (null distributions represented by gray bars).

DISCUSSION

Geographic distribution patterns

Both species present discontinuous patterns of distribution, with populations organized into different nuclei, mostly in elevated areas with high rainfall and cold climate, mainly in the Atlantic Forest. Although they present a large area of sympatry, they are probably not syntropic, since *G. brasiliensis* is mostly found in lentic waters, while *P. flavovirgatus* in lotic (Lema 2002, Menezes *et al.* 2018).

The discontinuous distribution pattern of *G. brasiliensis* may be explained (in 59.1%) by the most important environmental variables for this species: altitude (Alt) and minimum temperature in the coldest month (Bio 6). However, *G. brasiliensis* is usually found at higher elevations (up to 1,300 m a.s.l.), where most areas are marked by high rainfall and subtropical climate. We assume these variables, especially altitude (topographic) may act as environmental filters, which influence and delimit the distribution of this species. However, its presence in the DF is remarkable, since the location is situated in the ‘Cerrado’, a savanna-like domain in central Brazil, and far from the core populations of the species. Only a few specimens were collected in this area (see Prudente & Brandão 1998, Gonzalez *et al.* 2014), which may indicate a remnant isolated population. Several studies in the Atlantic

Forest point to the existence of phylogeographic discontinuities for numerous vertebrate taxa (Carnaval & Moritz 2008, Resende *et al.* 2010, Batalha-Filho & Miyaki 2011), supporting the "theory of refugia" (Vanzolini & Williams 1970) as a main hypothesis to explain such diversity. These areas were dense humid forest "islands" isolated by open vegetation; which they were retracted during periods of maximum glacial (forming refugia) and would expand during warmer periods (interglacials), while areas of open vegetation behaved otherwise (Batalha-Filho & Miyaki 2011). Thereby, species dependent on forest environments would have accompanied these cycles of forests (contraction and expansion) in the Pleistocene, causing diversification on the populations of different refugium by allopatry, if the insulation had enough time to accumulate differences (Batalha-Filho & Miyaki 2011).

On the other hand, the distribution pattern of *P. flavovirgatus* was also mainly explained (48.7%) by the same environmental variables: altitude (Alt) and minimum temperature in the coldest month (Bio 6), with a tendency to occur in highlands. The areas where this species occurs are colder than those of *G. brasiliensis* (Alvares *et al.* 2013). Populations are isolated by large gaps in SP (in the 'Serra da Mantiqueira') and SC (in the 'Serra Geral'). Intriguingly, *P. flavovirgatus* was never recorded in SP state (Porto & Caramaschi 1988, Gonzalez *et al.* 2014, Nogueira *et al.* 2019), despite intensive collection efforts in the region (Thomas *et al.* 2006, Zaher *et al.* 2011, Franco 2012, Moura *et al.* 2018). Similarly, the SC state, also relatively populous, has also had collection efforts but no reports of the species so far (*e.g.* Ghizoni-Jr. *et al.* 2009, Kunz *et al.* 2011).

Many closely related snake species have similar patterns of distribution, with discontinuous groups from the Southern Brazilian Plateau, and the 'Mantiqueira-Bocaina-Órgãos' mountain complex - *i.e.*: *Bothrops cotiara* and *B. fonsecai* (Franco *et al.* 2005, Morato *et al.* 2003, Tashima *et al.* 2008), *Clelia rustica* (Franco *et al.* 1997) and *C. hussami* (Morato *et al.* 2003), and *Pseudoboa serrana* and *P. haasi* (Morato *et al.* 1995, 2003). Moreover, the distribution pattern of *Ditaxodon taeniatus* is quite similar to *P. flavovirgatus*, being absent in most of SP state, while its distribution center seems to be in the Brazilian Southern Plateau, with records in the 'Serra da Mantiqueira', in Southeastern Brazil (Thomas *et al.* 2006).

Nogueira *et al.* (2019) undertook a massive effort to compile comprehensive information on the distribution of Brazilian snake species up to the point of their study's publication. Due to its extensive nature, this study can be regarded as a reference in the field. Nevertheless, details of each species' distributions (*i.e.* gaps) were not in the scope of this study, so many of them remain unstudied. Our findings play a role in the comprehension of both species' distribution patterns, thereby aiding more information in the assessment of their conservation status and monitoring.

Overlap of ecological niche models (ENMs)

The results of Bst for both indexes and directions also indicated more similarity of niches between the species than expected by chance. Therefore, here we corroborate both ecological interpretations on the predicted hypothesis of niches overlap between closely related species (Net and Bst). This way, all Bst results showed more niche similarity between *G. brasiliensis* and *P. flavovirgatus* than expected by chance, supporting the hypothesis of niche similarity of Peterson *et al.* (1999). In addition, we suggest an evolution of conserved environmental niche, as expected for closely related species, which would be associated with sympatry of related forms in a given region. However, ecological differentiation between species may reflect habitat availability in their respective regions, rather than an actual change in habitat preferences (Warren *et al.* 2008). While overlapping measures between species may be informed by the tests of hypothesis, we observed that niche similarity corresponds to the large overlapping areas (also meaning shared environmental conditions) in the large sympatric areas in southeastern and southern Brazil.

We suggest that the Niche equivalence test (Net) in this study appears to be more sensitive to layers used for generating ENMs (see Warren *et al.* 2008). The ENMs tests are useful for describing broad patterns of niche divergence across multiple environmental axes within a clade because the hypothesis-testing methods do not require phylogenies. However, methods with community phylogenies (Webb *et al.* 2002, Silvertown *et al.* 2006, Johnson & Stinchcombe 2007) may be more appropriate for addressing questions about specific environmental factors that may favor the co-occurrence of species (see Warren *et al.* 2008, 2010). The Net and Bst overlaps observed between *G. brasiliensis* and *P. flavovirgatus* may also be explained phylogenetically by their close relationship within the Tachymenini clade (Zaher *et al.* 2009, 2019, Grazziotin *et al.* 2012, Pyron *et al.* 2013, Trevine *et al.* 2022). Despite the occurrence of *G. brasiliensis* in the 'Cerrado', both species are associated with natural grassy fields in the highlands of the Atlantic Forest, since their distribution patterns seem to be dependent on topographic (altitude) and climatic (temperature and precipitation) variables that influence the regional vegetation of this biome (Jellinek *et al.* 2004). The influences of altitude and temperature are known to be important local and regional ecological variables, and particularly, in many studies of reptiles (see Ashton & Feldman 2003, Mesquita & Colli 2003, Angilletta *et al.* 2004, Cruz *et al.* 2005, Olalla-Tárraga *et al.* 2006, Costa *et al.* 2008, Terribili 2009).

Ecological considerations for conservation

Both species studied here share some attributes that may be concerning for their conservation: they have restricted distribution in the Atlantic Forest, where they live in freshwater in elevated areas, and which are largely coincident with the most populous areas of the country. They seem to be rare in nature, with few records in zoological collections, making it difficult to study them to understand basic aspects of their natural history (*i.e.* diet and reproduction), except for a few studies (*e.g.*, Menezes *et al.* 2017, 2018). This scenario pictures a very fragile situation in which both species may be at risk in their natural occurrence areas because of the niche they explore.

Obviously, the shortage of information on the basic biology of species has a direct impact on the assessment of their conservation statuses. *G. brasiliensis* and *P. flavovirgatus* have fairly incomplete profiles in the IUCN, where they are listed as "Least Concern" (LC) (Silveira *et al.* 2019a, b, IUCN 2022). Likewise, both are also considered "LC" in Brazil (ICMBio 2018) and none are cited in the national list of endangered species (Brazil 2022). We understand the difficulties in reaching the assessment results and hope future research will increase the amount of information about the natural history of both species, consequently helping their future reassessments. Models of distribution predicted a large number of threatened DD (Deficient Data) reptile species in the highly threatened Atlantic Forest (Böhm *et al.* 2013, Bland & Böhm 2016). Regrettably, many forest reptile species, of which little is known, may be threatened at this moment (Barreto-Lima & Simoncini 2019), including both species studies herein. Our study shed some light onto the real and potential distribution patterns of these snakes, addressing the most important abiotic factors that can be responsible for determining these patterns. We showed the existence of ecological niche overlap between them, showing that closely related species may still share some ecological preferences.

ACKNOWLEDGMENTS

We are grateful to Angele Martins, Bruno Miranda, Frederico de Alcântara Menezes, Manoela Woitovicz Cardoso, Paulo Machado, Pedro Pinna, and Vivian Ribeiro for lab support, and valuable suggestions. For the access to collection specimens, we thank Francisco Luis Franco, Gláucia Pontes, Guarino Colli, Hussam Zaher, Ivo Ghizoni-Jr., Julio Cesar de Moura-Leite, Moema Leitão de Araújo, Paulo Passos, Renato N. Feio, Ronaldo Fernandes, and Tobias Kunz. We also would like to thank: Axel Kwet and Frederico de Alcântara Menezes for the photographs of living specimens. RCG thanks Fundação de Desenvolvimento Administrativo/FUNDAP (process: 49498/10-6) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico/CNPq (process: 142370/2014-2) for financial support for financial support to examine several Brazilian herpetological collections. AFBL thanks the Ministério da Ciência, Tecnologia e Inovação (MCTI), CNPq research grant (process: 301328/2023-04), Programa de Capacitação Institucional (PCI), and the Instituto Nacional da Mata Atlântica (INMA) for the support.

REFERENCES

Aguirre-Gutiérrez, J., Serna-Chavez, H.M., Villalobos-Arambula, A.R., Perez de la Rosa, J.A., & Raes, N. 2015. Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines. Diversity and Distributions 21(3), 245–257. DOI: 10.1111/ddi.12268.

Alvares, C.A., Stape, J. L., Sentelhas, P.C., Gonçalves, J.L., & Sparovek, M.G. 2013. Köppen's climate classification map for Brazil. Meteoroligsche Zeitschrift 22(6), 711–728. DOI: 10.1127/0941-2948/2013/0507

Angilletta, M.J., Niewiarowski, P.H.Jr., Dunham, A.E., Leaché, A.D., & Porter, W.P. 2004. Bergmann's Clines in Ectotherms: Illustrating a Life–History Perspective with Sceloporine Lizards. American Naturalist 164(6), E168-E183.

Araujo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A.,Valladares, F., & Chown, S.L. 2013. Heat freezes niche evolution. Ecology Letters 16(9), 1206–1219. DOI: 10.1111/ele.12155

Ashton, K.G. & C.R. Feldman. 2003. Bergmann's rule in non avian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57 (5): 1151-1163.

Barreto-Lima A.F., & Simoncini, M.S. 2019. Forests and Brazilian reptiles: challenges for conservation. In: P. Eisenlohr (org.), Forest conservation: methods, management and challenges. pp. 67–110. New York: Nova Science Publishers.

Batalha-Filho, H., & Miyaki, C.Y. 2011. Phylogeography of the Atlantic Forest. Revista da Biologia 7(1), 31–34. DOI: 10.7594/revbio.07.06

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F., Bastos, R.P., & Pinto, M.P. 2006. Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. Diversity and distributions 12(5), 475–482. DOI: 10.1111/j.1366-9516.2006.00286.x

Bland, L.M. & Böhm, M. 2016. Overcoming data deficiency in reptiles. Biological Conservation 204(1), 16–22. DOI: 10.1016/j.biocon.2016.05.018

Bocard, D.P., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045-1055.

Böhm, M., Collen, B., Baillie, J.E., Bowles, P., Chanson, J., Cox, N., *et al.* 2013. The conservation status of the world's reptiles. Biological Conservation 157, 372–385. DOI: 10.1016/j.biocon.2012.07.015

Brazil. Ministério do Meio Ambiente. 2022. Portaria GM/MMA nº 300, de 13 de Dezembro de 2022. Lista Nacional de Espécies Ameaçadas de Extinção. Diário Oficial da União 234, 1–90.

Burnham, K.P., & Anderson, D,R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer–Verlag. New York.

Carnaval, A.C., & Moritz, C. 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. Journal of Biogeography 35(7), 1187–1201. DOI: 10.1111/j.1365-2699.2007.01870.x

Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333(6045), 1024–1026. DOI: 10.1126/science.1206432

Costa, H.C., Rezende, D.T., Molina, F.B., Nascimento, L.B., Leite, F.S.F., & Fernandes, A.P.B. 2015. New distribution records and potentially suitable areas for the threatened Snake-Necked Turtle *Hydromedusa maximiliani* (Testudines: Chelidae). Chelonian Conservation and Biology 14(1), 88–94. DOI: 10.2744/ccab-14-01-88-94.1

Costa G.C., Wolfe C., Shepard D.B., Caldwell, J.P., & Vitt, L.J. 2008. Detecting the influence of climatic variables on species distributions: a test using GIS niche–based models along a steep longitudinal environmental gradient. Journal of Biogeography 35, 637-646.

Cox, N., Young, B.E., Bowles, P. *et al.* 2022. A global reptile assessment highlights shared conservation needs of tetrapods. Nature 605(2022), 285–290. DOI: 10.1038/s41586-022-04664-7

Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E., & Schulte, J.A. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. Journal of Evolutionary Biology 18, 1559-1574.

Driscoll, D.A. 2004. Extinction and outbreaks accompany fragmentation of a reptile community. Ecological Applications 14(1), 220–240. DOI: 10.1890/02-5248

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E., & Yates, C.J. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17(1), 43–57. DOI: 10.1111/j.1472-4642.2010.00725.x

Fortes, V.B., Lucas, E.M., & Caldart. V.M. 2010. Reptilia, Serpentes, Dipsadidae, *Gomesophis brasiliensis* (Gomes, 1918): distribution extension in state of Santa Catarina, Brazil. Check List 6(3), 414–415. DOI: 10.15560/6.3.414

Franco, F.L. 2012. A Coleção Herpetológica do Instituto Butantan: da sua origem ao incêndio ocorrido em 15 de maio de 2010. Herpetologia Brasileira 1(1), 22–31.

Franco, F.L., Germano, V.J. & Martão, L.R. 2005. Notas sobre o lectótipo de *Bothrops cotiara* (Gomes, 1913) (Serpentes, Viperidae). Phyllomedusa 4(1), 75–78. DOI: 10.11606/issn.2316-9079.v4i1p75-78

Franco, F.L., Marques, O.A.V., Puorto, G. 1997. Two new species of colubrid snakes of the genus *Clelia* from Brazil. Journal of Herpetology 31(4), 483–490. DOI: 10.2307/1565599

Franklin, J. 2010. Mapping species distributions - spatial inference and prediction. Cambridge: Cambridge University Press. p. 320. DOI: 10.1017/CBO9780511810602.

Ghizoni-Jr., I.R., Kunz, T.S., Cherem, J.J. & Bérnils, R.S. 2009. Registros notáveis de répteis de áreas abertas naturais do planalto e litoral do Estado de Santa Catarina, sul do Brasil. Biotemas 22(3), 129–141.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., *et al.* 2000. The global decline of reptiles, déjà vu amphibians: reptile species are declining on a global scale. BioScience 50(8), 653–666. DOI:10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2

Gonzalez, R.C., Prudente, A.L.C & Franco, F.L. 2014. Morphological variation and distribution of *Gomesophis brasiliensis* Hoge and Mertens, 1959 and *Ptychophis flavovirgatus* Gomes, 1915 (Serpentes, Dipsadidae, Xenodontinae). Salamandra 50(2), 85–98.

Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J., & Moritz, C. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58(8), 1781–1793. DOI: 10.1554/03-274

Grazziotin, F.G., Zaher, H., Murphy, R.W., Scrocchi, G., Benavides, M.A., Zhang, Y., & Bonatto, S.L. 2012. Molecular phylogeny of the new world Dipsadidae (Serpentes: Colubroidea): a reappraisal. Cladistics 28(5), 1–23. DOI: 10.1111/j.1096-0031.2012.00393.x

Hawkins, B.A. 2004. Invited views in basic and applied ecology: Are we making progress toward understanding the global diversity gradient? Basic and Applied Ecology 5(1), 13. DOI: 10.1078/1439-1791-00214

Horváth, Z., Ptacnik, R., Vad, C.F., & Chase, J. M. 2019. Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. Ecology Letters 22(6), 1019–1027. DOI: 10.1111/ele.13260

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., Ferreira, L.G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensins of Environment 83(1–2), 195–213. DOI: 10.1016/S0034-4257(02)00096-2

IBGE (Instituto Brasileiro de Geografia e Estatística) 2023. IBGE Cidades. Retrieved on 9th June 2023, from https://cidades.ibge.gov.br

ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade). 2018. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção, v. 4: Répteis. Brasília: Instituto Chico Mendes de Conservação da Biodiversidade: p. 252.

IUCN (International Union for Conservation of Nature). 2022. The IUCN red list of threatened species. Retrieved on 28th November 2023, from https://www.iucnredlist.org

Jellinek, S., Driscolll, D.A., & Kirkpatrick, J. B. 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. Austral Ecology 29(3), 294–304. DOI: 10.1111/j.1442-9993.2004.01366.x

Johnson, M.T.J., Stinchcombe, J. R. 2007. An emerging synthesis between community ecology and evolutionary biology. Trends in Ecology and Evolution 22(5), 250–257. DOI: 10.1016/j.tree.2007.01.014

Kunz, T.S., Ghizoni-Jr., I.R., Giasson, L.O.M. 2011. Novos registros de répteis para as áreas abertas naturais do planalto e do litoral sul de Santa Catarina, Brasil. Biotemas 24(3), 59–68.

Menke, K., G.I.S.P., Smith Jr, R., Pirelli, L., & Van Hoesen, J. G.I.S.P. 2016. Mastering QGIS. 2nd Edition. Mumbai: Packt Publishing Ltd. p. 486.

Mesquita, R., & Colli, G.R. 2003. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). Copeia (2), 285-298.

Lema, T. 1967. Novo gênero e espécie de serpente opistoglifodonte do Brasil meridional ("Colubridae", "Colubrinae"). Iheringia 35(1), 61–67.

Lema, T. 2002. Os répteis do Rio Grande do Sul: atuais e fósseis, biogeografia, ofidismo. Porto Alegre: EDIPUCRS: p. 162.

Lema, T., Deiques, C.H. 1992. Contribuição ao conhecimento da "Cobra Espada D'água", *Ptychophis flavovirgatus* Gomes, 1915 (Serpentes, Colubridae, Xenodontinae, Tachymenini). Comunicações do Museu de Ciências e Tecnologia da PUCRS 5(6), 55–83.

Lisle, R. J. 2006. Google Earth: a new geological resource. Geology Today 22(1), 29–32.

Lomolino, M.V. 2004. Conservation biogeography. In M.V. Lomolino & L.R. Heaney (Eds.), Frontiers of Biogeography: new directions in the geography of nature. pp. 293–296. Sunderland: SinauerAssociates.

Marques, O.A.V., A. Eterovic, Sazima, I. 2001. Serpentes da Mata Atlântica – guia ilustrado para a Serra do Mar. Ribeirão Preto: Holos Editora: p. 184.

Marques, O.A.V., Eterovic, A., & Sazima, I. 2004. Snakes of the Brazilian Atlantic Forest: an illustrated field guide for the Serra do Mar range. Ribeirão Preto: Holos Editora: p. 206.

Marques, O.A.V., Nogueira, C., Martins, M., & Sawaya, R.J. 2010. Impactos potenciais das mudanças propostas no Código Florestal Brasileiro sobre os répteis brasileiros. Biota Neotropica 10(4), 39–42. DOI: 10.1590/S1676-06032010000400004

Marques, O.A.V., Nogueira, C., Sawaya, R.J., Bérnils, R.S., Martins, M., Molina, F., Ferrarezzi, H., Franco, F.L., Germano, V. J. 2009. Répteis. In P.M. Bressan, M.C.M. Kierulff & A.M. Sugieda (Orgs.), Livro vermelho da fauna ameaçada de extinção do Estado de São Paulo. pp. 285–327. São Paulo: Fundação Parque Zoológico de São Paulo, Secretaria do Meio Ambiente.

Menezes, F.A, Abegg, A.D., Da Silva, B.R., Franco, F.L., Feio, R.N. 2018. Composition and natural history of the snakes from the Parque Estadual da Serra do Papagaio, southern Minas Gerais, Serra da Mantiqueira, Brazil. ZooKeys, 797, 117–160.

Menezes, F.A., Fiorillo, B.F., Franco, F.L., & Feio, R.N. 2017. Repertoire of antipredator displays in the poorly known Atlantic forest snake, *Gomesophis brasiliensis* (Gomes, 1918). Herpetology Notes 10(2017), 245–247.

Miranda, E.A., Carvalho, A.F., Andrade-Silva, A.C.R., Silva, C.I., & Del Lama, M.A. 2015. Natural history and biogeography of *Partamona rustica*, an endemic bee in dry forests of Brazil. Insectes Sociaux, 62 (2015), 255–263. DOI: 10.1007/s00040-015-0400-z

Morato, S.A.A., Franco, F.L., & Sanches, E.J. 2003. Uma nova espécie de *Clelia* (Serpentes, Colubridae) do sul do Brasil. Phyllomedusa 2(2), 93–100. DOI: 10.11606/issn.2316-9079.v2i2p93-100

Morato, S.A.A., Moura-Leite, J.C., Prudente, A.L. C., & Bérnils, R.S. 1995. A new species of *Pseudoboa* Schneider, 1801 from southeastern Brazil (Serpentes: Colubridae: Xenodontinae: Pseudoboini). Biociências 3(2), 253–264.

Moura, M.R., Costa, H.C., Peixoto, M.A., Carvalho, A.L., Santana, D.J. & Vasconcelos, H.L. 2018. Geographical and socioeconomic determinants of species discovery trends in a biodiversity hotspot. Biological Conservation 220(2018), 237–244. DOI: 10.1016/j.biocon.2018.01.024

Nogueira C.C., Argôlo A.J.S., Arzamendia V., Azevedo J.A., Barbo F.E., Bérnils R.S., *et al.* 2019. Atlas of Brazilian snakes: Verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. South American Journal of Herpetology 14(sp1), 1–274. DOI: 10.2994/SAJH-D-19-00120.1

Olalla–Tárraga, M., Rodríguez, & M., Hawkins, B.A. 2006. Broad–scale patterns of body size in squamate reptiles of Europe and North America. Journal of Biogeography 33, 781-793.

Oliveira-Dalland, L.G., Alencar, L.R.V., Tambosi, L.R., Carrasco, P.A., Rautsaw, R.M., Jesus, S.R., Manfrini, G.J.S., & Martins, M. 2022. Conservation gaps for Neotropical vipers: Mismatches between protected areas, species richness and evolutionary distinctiveness. Biological Conservation 275. 10.1016/j.biocon.2022.109750

Oliveira, U., Paglia, A.P., Brescovit, A.D., de Carvalho, C.J.B., Silva, D.P., Rezende, D.T., *et al.* 2016. The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. Diversity and Distributions 22(12), 1–13. DOI 10.1111/ddi.12489

Peterson, A. T., Soberon, J., & Sanchez-Cordero, V. 1999. Conservatism of ecological niches in evolutionary time. Science 285(5431), 1265–1267. DOI: 10.1126/science.285.5431.1265

Phillips, S. J., Anderson, R.P., & Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190(3–4), 231–259. DOI: 10.1016/j.ecolmodel.2005.03.026

Porto, M., & Caramaschi, U. 1988. Notes on the taxonomic status, Biology, and distribution of *Ptychophis* *flavovirgatus* Gomes, 1915 (Ophidia, Colubridae). Revista Brasileira de Biologia 60, 471–475.

Prudente, A.L.C., & Brandão, R.A. 1998. Geographic Distribution. *Gomesophis brasiliensis*. Herpetological Review 29, 112.

Pyron, R.A., Burbrink, F.T., & Wiens, J.J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13, 93. DOI: 10.1186/1471-2148-13-93

Resende, H.C., Yotoko, K.S.C., Delabie, J.H.C., Costa, M.A., Campiolo, S., Tavares, M.G., Campos, L.A. O. & Fernandes-Salomão, T.M. 2010. Pliocene and Pleistocene events shaping the genetic diversity within the central corridor of the Brazilian Atlantic Forest. Biological Journal of the Linnean Society 101(4), 949–960. DOI: 10.1111/j.1095-8312.2010.01534.x

Sabaj, M.H. 2020. Codes for natural history collections in ichthyology and herpetology. Copeia 108(3), 593–669. DOI: 10.1643/ASIHCODONS2020

Silveira, A.L., Prudente, A.L.C., Argôlo, A.J.S., Abrahão, C.R., Nogueira, C., Strüssmann, *et al*. 2019a. *Gomesophis brasiliensis*. The IUCN Red List of Threatened Species 2019: e.T96105905A123740860. Retrieved on 18th May 2023, from https://dx.doi.org/10.2305/IUCN.UK.2019-2.RLTS.T96105905A123740860.en.

Silveira, A.L., Prudente, A.L.C., Argôlo, A.J.S., Abrahão, C.R., Nogueira, C., Strüssmann, *et al*. 2019a. *Ptychophis flavovirgatus*. The IUCN Red List of Threatened Species 2019: e.T15182432A123737562. Retrieved on 18th May 2023, from https://dx.doi.org/10.2305/IUCN.UK.2019-2.RLTS.T15182432A123737562.en

,

Schoener, T.W. 1968. *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49(4), 704–726. DOI: 10.2307/1935534

Tashima, A.K., Sanz, L., Camargo, A.C.M., Serrano, S.M.T., & Calvete, J.J. 2008. Snake venomics of the Brazilian pitvipers *Bothrops cotiara* and *Bothrops fonsecai*. Identification of taxonomy markers. Journal of Proteomics 71(4), 473–485. DOI: 10.1016/j.jprot.2008.07.007

Terribili, L.V. 2009. Padrões ecológicos globais de dois clados de serpentes, Viperidae e Elapidae (Squamata, Serpentes). Doctoral thesis, Universidade de São Paulo, Brazil, 212 p.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, *et al*. 2004. Extinction risk from climate change. Nature, 427(2004), 145–148. DOI: 10.1038/nature02121

Thomas, R.A., Bérnils, R.S., Moura-Leite, J.C., & Morato, S.A.A. 2006. Redescription of *Ditaxodon taeniatus* (Hensel, 1868) (Serpentes, Colubridae, Xenodontinae): variation, relationships, and distribution. South American Journal of Herpetology 1(2), 94–101. DOI: 10.2994/1808-9798(2006)1[94:RODTHS]2.0.CO;2

Trevine, V.C., Grazziotin, F.G., Giraudo, A., Sallaberry-Pincheira, N., Vianna, J.A., & Zaher, H. 2022. The systematics of Tachymenini (Serpentes, Dipsadidae): An updated classification based on molecular and morphological evidence. Zoologica Scripta, 51(6), 643–663. DOI: 10.1111/zsc.12565

Van der Vaart, A. W. 1998. *Asymptotic statistics*. Cambridge. Cambridge University Press. 903 pp. https://doi.org/10.1017/CBO9780511802256

Vanzolini, P.E., & Williams, E.E. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria: Iguanidae). Arquivos de Zoologia 19(1–2), 1–298. DOI: 10.11606/issn.2176-7793.v19i1-2p1-176

Wallach, V., Williams, K.L., & Boundy, J. 2014. Snakes of the world. A catalogue of living and extinct species. Boca Raton: CRC Press: p. 1237. DOI: 10.1201/b16901

Warren, D.L., Glor, R.E., & Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62(11), 2868–2883. DOI: 10.1111/j.1558-5646.2008.00482.x

Warren, D. L., Glor, R.E., & Turelli, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33, 607–611. DOI: 10.1111/j.1600-0587.2009.06142.x.

Webb, C.O., Ackerly, D.D., McPeek, M.A., & Donoghue, M.J. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33(2002), 475–505. DOI: 10.1146/annurev.ecolsys.33.010802.150448

Whittaker, R.J., Araújo, M.B., Paul, J., Ladle, R.J., Watson, J.E.M., & Willis, K.J. 2005. Conservation biogeography: assessment and prospect. Diversity and Distributions, 11(1), 3–23. DOI: 10.1111/j.1366-9516.2005.00143.x

Zaher, H., Barbo, F.E., Martínez, P.S., Nogueira, C., Rodrigues, M.T., & Sawaya, R.J. 2011. Répteis do Estado de São Paulo: conhecimento atual e perspectivas. Biota Neotropica 11, 1–15. DOI: 10.1590/S1676-06032011000500005

Zaher, H., Grazziotin, F.G., Cadle, J.E., Murphy, R.W., Moura-Leite, J.C., & Bonatto, S.L. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. Papéis Avulsos de Zoologia 49, 115–153. DOI: 10.1590/S0031-10492009001100001

Zaher, H., Murphy, R.W., Arredondo, J.C., Graboski, R., Machado-Filho, P.R., Mahlow, K., *et al*. 2019. Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced Caenophidian snakes (Squamata: Serpentes). PloS One 14(5), e0216148. DOI: 10.1371/journal.pone.0217959

Zank, C., Becker, F.G., Abadie, M., Baldo, D., Maneyro, R., & Borges-Martins, M. 2014. Climate change and the distribution of neotropical red-bellied toads (*Melanophryniscus*, Anura, Amphibia): how to prioritize species and populations? PloS One 9, e94625. DOI: 10.1371/journal.pone.0094625

APPENDIX I

Material examined and literature records. Acronyms are cited here according to Sabaj (2020).

Submitted:28 June 2023
Accepted: 10 January 2024

Associate Editor: Gabriel Massaine Moulatlet