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Original Article

Climatic niche breadths of the Atlantic Forest snakes do not increase with increasing latitude

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Abstract

The climatic niche is a central concept for understanding species distribution, with current and past climate interpreted as strong drivers of present and historical-geographical ranges. Our aim is to understand whether Atlantic Forest snakes follow the general geographical pattern of increasing species climatic niche breadths with increasing latitude. We also tested if there is a tradeoff between temperature and precipitation niche breadths of species in order to understand if species with larger breadths of one niche dimension have stronger dispersal constraints by the other due to narrower niche breadths. Niche breadths were calculated by the subtraction of maximal and minimal values of temperature and precipitation across species ranges. We implemented Phylogenetic Generalized Least Squares to measure the relationship between temperature and precipitation niche breadths and latitude. We also tested phylogenetic signals by Lambda statistics to analyze the degree of phylogenetic niche conservatism to both niche dimensions. Temperature niche breadths were not related to latitude. Precipitation niche breadths decreased with increasing latitude and presented a high phylogenetic signal, that is, significant phylogenetic niche conservatism. We rejected the tradeoff hypotheses of temperature and precipitation niche breadths. Our results also indicate that precipitation should be an important ecological constraint affecting the geographical distribution of snake lineages across the South American Atlantic Forest. We then provide a general view of how phylogenetic niche conservatism could impact the patterns of latitudinal variation of climatic niches across this biodiversity hotspot.

Keywords: Atlantic Forest, biogeography, climatic niche, latitudinal gradient, snakes

Climate is one of the main ecological drivers of species distribution on broad scales (see MacArthur 1972; Wiens and Donoghue 2004; Chejanovski and Wiens 2014; Qian et al. 2015). The climatic tolerances of species lineages can promote restrictions of dispersal out from where the ancestors have emerged due to phylogenetic niche conservatism (Wiens and Donoghue 2004; Pyron and Burbrink 2009; Chejanovski and Wiens 2014). Phylogenetic niche conservatism is the trend for a phylogenetic lineage to retain its adaptive traits over evolutionary history (Holt and Gomulkiewicz 2004; Wiens et al. 2010). The trend to conserve evolutionary traits, including climatic tolerances, should constrain geographical distribution and, consequently, the variation in clade composition among different regions. Then, the geographical ranges of species can be determined by climatic niche breadths, or the interval between maximum and minimum values of temperature and precipitation in which lineages can occur and persist (Fisher-Reid et al. 2012; Slatyer et al. 2013; Bonetti and Wiens 2014; Chejanovski and Wiens 2014; Rolland and Salamin 2016).

Some studies have pointed out that species richness is strongly influenced by phylogenetic niche conservatism, with lineages tending to conserve ancestral climatic niche conditions along latitudinal gradients (Wiens and Donoghue 2004; Pyron and Burbrink 2009; Rivadeneira et al. 2011; Morinière et al. 2016). Phylogenetic niche conservatism generates a phylogenetic signal which can be detected when certain characters are conserved across the evolutionary history of a clade (Webb 2000; Kraft et al. 2007; Losos 2008; Cavender-Bares et al. 2009; Pausas and Verdú 2010; Mouquet et al. 2012). In this way, evolutionary drivers can limit the adaptive responses to different environmental conditions as well as restrict dispersal rates across adjacent areas (Wiens and Donoghue 2004; Pyron et al. 2015). Phylogenetic niche conservatism could also constrain the diversity along latitudinal gradients due to conserved climatic niche breadths in lineages adapted to climatic conditions in specific latitudinal ranges (Wiens and Donoghue 2004; Pyron and Burbrink 2009; Pyron et al. 2015). Thus, phylogenetic lineages can be restricted to latitudinal belts where their ancestors have emerged due to phylogenetic niche conservatism of climatic niches (Wiens and Donoghue 2004).

MacArthur (1972) suggests that species niche breadths increase with increasing latitude and decreasing climatic stability. Such niche breadth variation could be associated to lower niche overlaps in tropical regions, which in turn would

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support higher species richness by accelerating diversification processes in lower latitudes (MacArthur 1972; see also Kozak and Wiens 2007; Kozak and Wiens 2010; Fisher-Reid et al. 2012; Salisbury et al. 2012; Gómez-Rodríguez et al. 2015; Rolland and Salamin 2016). Kozak and Wiens (2007) pointed out 2 major influences on latitudinal gradients of species diversity: the species tolerances to climate variation along the latitudinal gradient and the isolation of lineages in mountain ranges due to smaller niche breadths (see also Janzen 1967). The Amazonian bird species demonstrated that the greater ecological specialization promotes dispersal limitation and higher speciation in lower latitudes (Salisbury et al. 2012). On the other hand, plethodontid salamanders evidenced that latitudinal variation trends should be present due to evolutionary processes regarding phylogenetic conservatism and geographical restrictions of dispersion throughout climatic zones, even in greater latitudes (Kozak and Wiens 2010). Additionally, both Salisbury et al. (2012) and Kozak and Wiens (2010) agree regarding the importance of evolutionary factors regulating latitudinal gradients. Thus, ecological and evolutionary approaches are crucial to understand latitudinal biodiversity gradients as proposed by MacArthur (1972).

Temperature could be a major influence for ectothermic vertebrate distribution along latitudinal gradients (Wiens and Donoghue 2004). Snake lineages also tend to be highly specialized on habitat use and ecological conditions such as thermal constraints (Greene and Greene 1997; Terribile et al. 2009). Moreover, a tradeoff has been suggested regarding temperature and precipitation conditions in broad-scale latitudinal gradients. While mean temperature ranges increase with latitude, the opposite must occur with precipitation, which could reflect in the species niche breadths (Currie 1991; Vázquez and Stevens 2004). In this way, even with a broad niche breadth regarding temperature, the opposite should occur with precipitation. Testing this tradeoff hypothesis on species niche data could provide foundations for understanding the influence of ecological specialization of clades and the niche axis associated with geographical restriction across different latitudes (Bonetti and Wiens 2014). Then, if species have broad niche breadths for temperature and lower niche breadths for precipitation, the major geographical constraint would be determined by precipitation niche breadths (Bonetti and Wiens 2014).

Bonetti and Wiens (2014) tested the tradeoff between temperature and precipitation niche breadths for amphibians. Those authors demonstrated that it would not be applicable to their species occurrence data, as they found congruence between temperature and precipitation niche breadths among localities. The congruence between temperature and precipitation niche breadths among such highly diversified lineages would be related to the diverse and specialized reproductive modes of amphibians (Bonetti and Wiens 2014). Terrestrial elapid snakes also present similar congruence on temperature and precipitation niche breadths related to clades' specialization in diverse climatic regimes along the globe (Lin et al. 2019). Lizards, on the other hand, show idiosyncratic responses to climatic factors related to differential geographical distribution of clades across the Atlantic Forest in South America (Prates et al. 2016). However, there is no available literature on climatic niche breadths distribution along latitudinal gradients for snakes (but see Lin et al. 2019 for terrestrial elapids in different regions).

The Atlantic Forest is a complex morphoclimatic domain, including different ecological constraints and conditions throughout its range (Olson et al. 2001; Carnaval et al. 2014). This region harbors a very diverse and highly endemic snake fauna, with at least 252 species, including 79 endemic snakes (Barbo et al. 2021). Carnaval et al. (2014) demonstrated that climate variation affects the geographical distribution of endemic vertebrates in the Atlantic Forest, including amphibians, lizards, snakes, and Passeriformes. Moreover, Moura et al. (2017b) reinforced such findings from Carnaval et al. (2014) indicating that the phylogenetic composition of snake species is strongly influenced by climate variation along the Atlantic Forest related to a general division between southern and northern faunas. Different climatic regimes can determine the ecological influence and different lineages' composition throughout the Atlantic Forest ecoregions, and such variation can influence the regionalization of snake diversity along the latitudinal gradient (Moura et al. 2017a, 2017b).

We tested herein if climatic niche breadths of species increase with increasing latitudes using the Atlantic Forest snakes as a model. We also tested the tradeoff between temperature and precipitation niche breadths. We implemented phylogenetic approaches to assess the phylogenetic niche conservatism for temperature and precipitation niche breadths. We hence provide a general view of how the evolutionary history of snake lineages and the possible niche conservatism could impact the patterns of latitudinal variation of climatic niches across the South American Atlantic Forest.

Materials and Methods

We analyzed the species composition of Atlantic Forest and extracted occurrence points from the most detailed voucher-based dataset of point locality records for snakes in Brazil (Nogueira et al. 2019). We estimated the phylogenetic relationships of species from 100 trees derived from fully sampled phylogenies for Squamate reptiles available in Tonini et al. (2016). From the 250 species occurring in the Atlantic Forest ecoregions (*sensu* Olson et al. 2001) according to Nogueira et al. (2019), we excluded species with less than 10 records, island endemics, and missing species from the phylogeny, resulting in 189 species (see the complete species list in Supplementary Materials S1).

We determined the mean latitudinal point from the non-repeated occurrence points for each species. Then, we extracted the climatic variable values at a fine resolution (1 km^2) from CHELSA database (Karger et al. 2017) for each nonrepeated occurrence point of each species in the *raster* R package (Hijmans et al. 2015). Niche breadths were calculated by subtracting the minimum temperature of the coldest month from the maximum temperature of the warmest month, and the minimum precipitation values of the driest quarters of the year from the maximum precipitation values of the wettest quarters (see Quintero and Wiens 2013). In this way, we obtained temperature niche breadths and precipitation niche breadths for each snake species of the Atlantic Forest (available in Supplementary Material). We also tested spatial autocorrelation among latitudinal belts and niche breadths with Moran's Index ($P > 0.05$) in the *ape* R package (Paradis et al. 2015) (see Supplementary Materials S2).

We used phylogenetic generalized least squares ([PGLS]—Martins and Hansen 1997) to analyze the phylogenetic weight within the models (see also Felsenstein 1985; Garland and

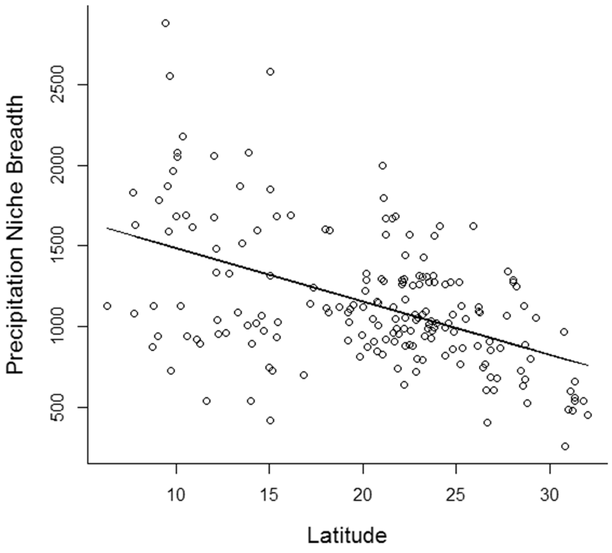

Figure 1. Relationship between precipitation niche breadths and mean latitude of Atlantic Forest snakes (N = 189 species) from 3 to 33° south (R^2 = 0.21, $P < 0.01$ in the PGLS model).

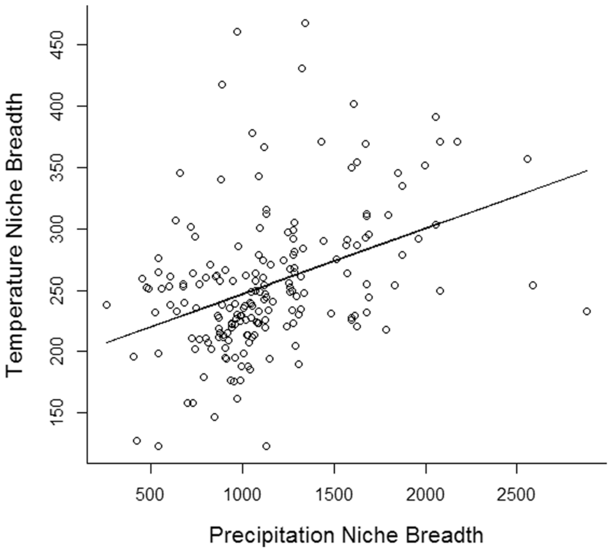

Figure 2. Relationship between temperature and precipitation niche breadths of Atlantic Forest snakes (N = 189 species) (R^2 = 0.14, $P < 0.01$ in the PGLS model).

Ives 2000; Quintero and Wiens 2013) in the *caper* R Package (Orme et al. 2018). This method identifies phylogenetic correlations on the distribution of traits throughout environmental gradients, such as the distributions of climatic niche breadths across the Atlantic Forest latitudinal gradient (Quintero and Wiens 2013). The λ values were estimated by the maximum likelihood and kappa and delta fixed at 1 for all PGLS models (Lin et al. 2019).

We also calculated the Lambda statistic (Pagel 1992) to measure the degree of phylogenetic conservatism for climatic niche breadths. The lambda values vary between 0, indicating no phylogenetic signal, to 1, or maximum phylogenetic signal of the analyzed trait. All phylogenetic approaches were repeated 100 times for each phylogeny and average values were considered. All analyses were performed in R software 4.1.1 (R Development Core Team 2020).

Results

The PGLS model indicates a positive relationship between latitude and temperature niche breadths variation across the gradient, but with a low explanatory power and without phylogenetic influence in the model (R^2 = 0.04, $P < 0.01$, slope = 2.02, $\lambda < 0.01$). Precipitation niche breadths were negatively related to latitude (R^2 = 0.21, $P < 0.01$, slope = –30.19, λ = 0.34; Figure 1). Temperature and precipitation niche breadths showed a positive relationship in the PGLS model (R^2 = 0.14, $P < 0.01$, slope = 2.58, λ = 0.54; Figure 2). The lambda statistics regarding the niche attributes indicated the absence of a phylogenetic signal on temperature niche breadths ($\lambda < 0.01$, $P > 0.01$), and a significant phylogenetic signal for precipitation niche breadths (λ = 0.61, $P < 0.01$).

Discussion

We rejected both hypotheses of climatic niche breadths increasing in higher latitudes (MacArthur 1972) and the tradeoff between temperature and precipitation niche breadths as proposed by Vázquez and Stevens (2004). Actually, temperature and precipitation niche breadths were correlated for the Atlantic Forest snakes, with a significant phylogenetic weight (λ = 0.54) in the PGLS model. Our finding is in line with those from Quintero and Wiens (2013) for plethodontid salamanders, hylid frogs, and phrynosomatid lizards on the congruence of climatic niche breadths and the absence of tradeoff between them. We also provided similar results as those found for terrestrial elapid snakes from different regions of the globe (Lin et al. 2019). The latitudinal gradient of precipitation niche breadths showed a strong phylogenetic signal. This result suggests that precipitation may be an important ecological constraint restricting the distribution of snake lineages across the Atlantic Forest.

MacArthur (1972) provided evidence that places with higher climatic stability and lower niche breadths can promote higher diversification. It would be due to higher species specialization in resource use related to a higher environmental heterogeneity observed in tropical landscapes. We recorded a higher concentration of points in the southeastern region of the Atlantic Forest, between 20 and 27° south, with species showing relatively narrow climatic niche breadths (see Figure 1). This can be also correlated with the higher historical climatic stability in the southern forested refugees to the Atlantic Forest fauna during the Late Quaternary (Carnaval et al. 2014). The historical variation of climatic conditions has been considered as a significant factor generating the current lineage distribution (Quintero and Wiens 2013). For instance, plethodontid salamanders demonstrate that specific environmental conditions such as high productivity and energy can promote rapid niche evolution, mainly where the climate is stable (Kozak and Wiens 2010). In this way, evolutionary factors could restrict species distributions due to the conservation of adaptive traits in specific climatic regimes, promoting the increasing number of species even with increasing latitude.

The southern richest areas are influenced by the historical and current climate, primary productivity, and energy availability highlighting the montane moist forests (see Moura et al. 2007a; Carnaval et al. 2014). The historical climate promoted higher forest stability at highlands in higher latitudes in the

Atlantic Forest, however, with great contemporary climatic heterogeneity (Carnaval et al. 2014). In this way, such climatic heterogeneity can be associated with physical and ecological factors including topography and vegetation structure in the Atlantic Forest (Moura et al. 2017a). Areas with higher historical stability and greater topographical complexity toward the south in the Atlantic Forest (Moura et al. 2017a, 2017b) would be also related to decreasing precipitation niche breadths found there. Species restricted to small geographic ranges could show limited tolerances for one climatic variable such as pluviosity, which can also promote congruence on limited temperature conditions (Lin et al. 2019). The lower tolerances for variation on climatic conditions could strengthen geographical barriers related to topographical variation along complex mountain ranges (see Kozak and Wiens 2007). Furthermore, such biogeographical barriers could favor reproductive isolation decreasing gene flow among populations and, consequently, promoting allopatric speciation (Kozak and Wiens 2007, 2010; Fisher-Reid et al. 2012; Salisbury et al. 2012; Gómez-Rodríguez et al. 2015; Rolland and Salamin 2016). The diversification rates among clades are highly related to climatic niche evolution and are associated with geographical isolation of taxa (Kozak and Wiens 2010). Such factors can also result in higher amphibian diversity on highly complex areas, highlighting the mountain ranges of southeastern Brazil (Vasconcelos et al. 2014). Such areas are also strongholds of higher species numbers of Atlantic Forest snakes and should have an important influence in our findings.

The higher number of Dipsadidae and Colubridae snake lineages in our sample (see Supplementary Appendix S1) should explain the higher phylogenetic signal effect in areas with lower precipitation niche breadths. Besides, the lambda value ($\lambda = 0.61$) does not show the maximum phylogenetic signal for precipitation and, consequently, provides evidence that phylogenetic niche conservatism would be related to younger lineages of snakes in the Atlantic Forest. The dispersal restrictions of these lineages could have generated a higher number of species specialized in specific ecological conditions regulated by climatic constraints across the latitudinal gradient. These younger lineages could be more influenced by their climatic preference of where their ancestors have emerged. In this way, these clades can be restricted to specific regions. In the case of the Atlantic Forest, this region of mountain ranges in the southeast has great environmental heterogeneity and provides conditions for allopatric speciation, which could be also regulated by phylogenetic niche conservatism (see Wiens 2004). Evolution is influenced by climate, which in turn can drive biogeographical patterns related to climatic niche breadth constraints, as already observed for amphibians and mammals (Olalla-Tárraga et al. 2011). More ancient clades of snakes, for instance, had more time to adapt to different ecological conditions, whereas more recent clades should suffer greater influence of phylogenetic niche conservatism. Thus, snakes of more recent divergences could provide better indicators of evolutionary constraints regarding climate preferences (Terribile et al. 2009).

The climatic variation in the Atlantic Forest demonstrates a simple division between northern and southern climatic regimes as 2 main “climatic spaces” (Carnaval et al. 2014) which must have influenced the snake composition (Moura et al. 2017b). Thermal constraints regulate species composition and phylogenetic beta diversity across this complex biome (Moura et al. 2017b). However, our results show that precipitation niche breadth is conserved across the evolutionary history of Atlantic Forest snakes. Precipitation should be an important ecological factor related to the geographical distribution of some lineages, possibly associated with the topographical variation and environmental heterogeneity. Thus, future approaches, exploring especially more recent lineages and different climatic dimensions, topographical and altitudinal variation along the Atlantic Forest ecoregions, could bring new insights on historical biogeography, ecology, and species richness variation across the Atlantic Forest.

We agree that snake composition throughout the Atlantic Forest range is strongly affected by sub-region variations (Moura et al. 2017a; Barbo et al. 2021). However, we complement herein the role of ecological and evolutionary drivers influencing the snake composition across this geographical domain. Our findings help to better understand how climatic factors could be related to biogeography and the evolution of the highly diversified snake fauna of the Atlantic rainforest. We emphasize that integrative approaches of such factors are important for a better understanding of the processes driving species distribution in biodiversity hotspots.

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Author Contributions

J.T.M.P. planned the study and analyzed the data. F.E.B. collected data. R.J.S. advised the study. All authors discussed the results and wrote the manuscript together.

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Conflict of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Supplementary Material

“Supplementary material can be found at https://academic.oup.com/cz”.

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