

## Richness and phylogenetic diversity are affected by space and time in the megadiverse Atlantic Forest of South America

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**ABSTRACT**

Understanding variation of species richness along latitudinal gradients, with more species toward the tropics, represents a challenge for ecologists. Species richness also varies according to the available area, with more species in larger regions, with area and latitude posited as major drivers of richness variations. However, species richness does not fully capture the evolutionary history behind those patterns. Phylogenetic diversity can provide insights on the role of time and evolutionary drivers of environmental gradients. We analyzed here the latitudinal gradient of endemic snakes from the Atlantic Forest of South America, a megadiverse and highly threatened portion of the Neotropics. We assessed the effect of area and average clade age on species richness and phylogenetic diversity, testing whether species richness and phylogenetic diversity increase with area availability and in lower latitudes. We found that area can predict species richness, but not phylogenetic diversity. Brazilian southeastern mountain ranges include larger patches of Atlantic Forest and the highest richness levels, but generally harboring snakes from relatively recent clades (neoendemics). There is a negative relationship between species richness and average clade age along the latitudinal gradient, with older clades found mainly in northern portions, increasing phylogenetic diversity at lower latitudes. Different dimensions of diversity, species richness and phylogenetic diversity, are thus affected in different ways by area and time for speciation in the Atlantic Forest, and this may be a trend in highly diverse tropical regions.

## INTRODUCTION

Biodiversity distribution can be influenced by geographical extent, position and evolutionary time. Species richness can be strongly affected by available area, with larger regions tending to contain more species (Hortal et al., 2009; Parent, 2012). One of the reasons is that more habitat diversity can be present in larger areas, where more species can co-occur (Hortal et al., 2009). Richer areas tend to harbor older clades due to more time for speciation and/or higher diversification rates (Wiens & Donoghue, 2004; Pyron & Burbrink, 2009; Wiens, 2012). Richer areas are also often found close to the equator, at lower latitudes, resulting in a latitudinal gradient of species richness, a general biogeographical pattern across the globe. Latitudinal gradient of species richness, or the increase of richness with decreasing latitude, is one of the most largely explored biogeographical patterns (MacArthur, 1972; Gaston, 2000; Brown, 2014; Kerkhoff, Moriarty & Weiser, 2014). Explanations for megadiverse tropical biotas may depend on complex interactions among latitude, time for speciation and available area, with tropical environments in lower latitudes being often larger and older than temperate environments (Wiens & Donoghue, 2004; Wiens, 2012).

However, the number of species alone does not encompass all factors driving biogeographical patterns. Additional components of diversity, such as phylogenetic diversity, can reveal how phylogenetic relationships and evolutionary time affect species richness across environmental gradients. Phylogenetic diversity can be considered as the sum of branch lengths of phylogenetic relationships in ecological communities or biotas (Faith, 1992). Thus, phylogenetic diversity can enhance our understanding of drivers of biodiversity across space and evolutionary history (Wiens & Donoghue, 2004; Pyron & Burbrink, 2009; Qian et al., 2015).

One of the explanations for the distribution of clades along latitudinal gradients is the “tropical niche conservatism” hypothesis (Wiens & Donoghue, 2004). This hypothesis is based on the assumption that most clades have tropical origins and phylogenetic niche conservatism would be prevalent. The phylogenetic niche conservatism is the trend for each phylogenetic lineage to retain adaptive traits along their evolutionary history (Holt & Gomulkiewicz, 2004; Wiens et al., 2010). It can

constrain the range of a given lineage to ancestral latitudes of that particular clade, due to adaptive traits related to specific climatic conditions (Wiens & Donoghue, 2004; Pyron & Burbrink, 2009). Under the same scenario, inverse latitudinal gradients are present when clades have a temperate origin (see Pyron & Burbrink, 2009; Rivadeneira et al., 2011; Morinière et al., 2016), retaining a temperate range along its evolutionary history.

In this way, the term “biogeographical niche conservatism” (*sensu* Pyron & Burbrink, 2009) could integrate both tropical and temperate origin of the clades, with the same premises of evolutionary time effect (Pyron & Burbrink, 2009; Rivadeneira et al., 2011; Morinière et al., 2016). Thus, area availability and age of clades are important factors driving species richness and phylogenetic diversity along latitudinal gradients (Wiens & Donoghue, 2004; Pyron & Burbrink, 2009). Thus, species richness and phylogenetic diversity would be higher near the region of origin (majoritarily in the tropics) due to older age and higher diversification rates in these areas (Wiens & Donoghue, 2004; Romdal, Araújo & Rahbek, 2013; Kerkhoff, Moriarty & Weiser, 2014).

The distinct geographical origins of different clades have been suggested to influence snake diversity in the Neotropical region (see Cadle & Greene, 1993). The Atlantic Forest is one of the richest areas in the Neotropics, harboring one quarter of the endemic species of the 25 global biodiversity conservation hotspots (Myers et al., 2000). The Atlantic Forest is highly threatened by habitat loss, having lost around 90% of its original forest cover (see Myers et al., 2000; Ribeiro et al., 2009; Ribeiro et al., 2011), and spans around 29 degrees of latitude in an area around 150.000.000 ha (Ribeiro et al., 2009).

We tested here how area and evolutionary time are related to endemic snake richness and phylogenetic diversity along the latitudinal gradient of the Atlantic Forest. We first assessed whether species richness decreases with increasing latitude. We then tested premises of “biogeographical niche conservatism” hypothesis, assessing the role of area and average clade age on species richness and phylogenetic diversity. Our major aim is to promote a better understanding of the ecological and evolutionary

drivers of biodiversity in the Atlantic Forest of South America, and to provide clues on the evolution of megadiverse tropical ecosystems.

## MATERIALS & METHODS

We used a dataset of Neotropical snake records housed in museums during the last 150 years, encompassing 147,515 records of 886 species with maps of one degree resolution (Guedes et al., 2018). We selected endemic snakes of the Atlantic Forest region (*sensu* Olson et al., 2001). We then summed raster files to calculate species richness of endemic snakes in the Atlantic Forest of South America.

Evolutionary relationships were estimated from 100 phylogenetic trees derived from a fully sampled phylogeny for Squamate reptiles, available in Tonini et al. (2016). In this way, all phylogenetic approaches were implemented 100 times, and mean values were used. The only missing Atlantic Forest endemic species in phylogenies (*Thamnodynastes* cf. *nattereri*) was excluded from subsequent analyses. Phylogenetic diversity was calculated as the standardized diversity metric of Faith (1992), which is independent of species richness, in R package ‘PhyloMeasures’ (Tsirogiannis & Sandel, 2017).

To calculate average clade age, we pruned the phylogenies including only species found in each latitudinal degree, with function *prune.sample* of ‘picante’ R package (Kembel et al., 2018). We then determined the average age of endemic lineages in each latitudinal degree. Area was measured as the sum of raster cells in each degree of latitude across the Atlantic Forest (*sensu* Olson et al., 2001). We analyzed relationships among species richness, phylogenetic diversity, average clade age and area across the latitudinal gradient by linear and quadratic regressions (Wiens & Donoghue, 2004; Buckley et al., 2010; Kerkhoff, Moriarty & Weiser, 2014). All analyses were performed in R software (R Core Team, 2018).

## RESULTS

We recovered 69 endemic snakes belonging to eight families in the Atlantic Forest region (Table 1). Species richness was lower in lower latitudes, being concentrated in the Southeastern portion of Atlantic Forest. Richness presented a unimodal pattern with a peak between 22 and 24° degrees south (Fig. 1; Fig. 2A), fitted to a quadratic model ( $R^2 = 0.67$ ,  $p < 0.01$ ; Fig. 2A). Average clade age presented an inverse pattern, also fitted to a quadratic model ( $R^2 = 0.66$ ,  $p < 0.01$ ), with lower values between 25 and 29° degrees south (Fig. 2B). The relationship between area and species richness was also fitted by a quadratic model across the latitudinal gradient ( $R^2 = 0.51$ ,  $p < 0.01$ ), with highest richness between 21 and 24° degrees south (Fig. 2C). Northern areas presented higher values of phylogenetic diversity, despite lower values of species richness (Fig 1). Phylogenetic diversity increased at lower latitudes ( $R^2 = 0.30$ ,  $p < 0.01$ ), with highest values in 7, 8, 14, 15 and 17 degrees south (Fig. 2D).

**Table 1:** Species composition of endemic snakes from the Atlantic Forest ecoregion.

| Species/Family  |  |
|---|--|
| <b>Tropidophiidae</b>   | <i>Dipsas albifrons</i> (Sauvage 1884)                 |
| <i>Tropidophis grapiuna</i> (Curcio, Nunes, Argolo, Skuk & Rodrigues 2012)  | <i>Dipsas alternans</i> (Fischer 1885)                 |
| <i>Tropidophis paucisquamis</i> (Müller 1901)                               | <i>Dipsas sazimai</i> Fernandes, Marques & Argolo 2010 |
| <i>Tropidophis preciosus</i> (Curcio, Nunes, Argolo, Skuk & Rodrigues 2012) | <i>Echianthera amoena</i> (Jan 1863)                   |
| <b>Boidae</b>   | <i>Echianthera cephalomaculata</i> Di-Bernardo 1994    |
| <i>Corallus cropanii</i> (Hoge 1953)  | <i>Echianthera cephalostriata</i> Di-Bernardo 1996     |
| <b>Anomalepididae</b>   | <i>Echianthera cyanopleura</i> (Cope 1885)             |
| <i>Liotyphlops caissara</i> Centeno, Sawaya & Germano 2010                  | <i>Echianthera melanostigma</i> (Wagler 1824)          |
| <i>Liotyphlops trefauti</i> Freire, Caramaschi & Argolo 2007                | <i>Echianthera undulata</i> (Wied 1824)                |

**Leptotyphlopidae**

*Trilepida salgueiroi* (Amaral 1955)

**Viperidae**

*Bothrops alcatraz* Marques, Martins & Sazima 2002

*Bothrops cotiara* (Gomes 1913)

*Bothrops fonsecai* Hoge & Belluomini 1959

*Bothrops insularis* (Amaral 1921)

*Bothrops jararaca* (Wied 1824)

*Bothrops jararacussu* Lacerda 1884

*Bothrops leucurus* (Wagler 1824)

*Bothrops muriciensis* Ferrarezzi & Freire 2001

*Bothrops otavioi* Barbo, Grazziotin, Sazima, Martins & Sawaya 2012

*Bothrops pirajai* Amaral 1923

**Elapidae**

*Micrurus corallinus* (Merrem 1820)

*Micrurus decoratus* (Jan 1858)

**Dipsadidae**

*Atractus caete* Passos, Fernandes, Bérnils & Moura-Leite 2010

*Atractus francoi* Passos, Fernandes, Bérnils & Moura-Leite 2010

*Atractus guentheri* (Wucherer 1861)

*Atractus maculatus* (Günther 1858)

*Atractus potschi* Fernandes 1995

*Atractus ronnie* Passos, Fernandes & Borges-Nojosa 2007

*Atractus serranus* Amaral 1930

*Elapomorphus quinquelineatus* (Raddi 1820)

*Elapomorphus wuchereri* (Günther 1861)

*Erythrolamprus atraventer* (Dixon & Thomas 1985)

*Helicops carinicaudus* (Wied-Neuwied 1825)

*Mussurana montana* (Franco, Marques & Puerto 1997)

*Oxyrhopus clathratus* Duméril, Bibrón & Duméril 1854

*Oxyrhopus formosus* (Wied-Neuwied 1820)

*Philodryas arnaldoi* (Amaral 1932)

*Pseudoboa haasi* Boettger 1905

*Pseudoboa serrana* Morato, Moura-Leite, Prudente & Bérnils 1995

*Ptychophis flavovirgatus* Gomes 1915

*Sibynomorphus neuwiedi* (Ihering 1911)

*Siphlophis longicaudatus* (Andersson 1907)

*Siphlophis pulcher* (Raddi 1820)

*Sordellina punctata* (Peters 1880)

*Taeniophallus affinis* (Günther 1858)

*Taeniophallus bilineatus* (Fischer 1885)

*Taeniophallus persimilis* (Cope 1869)

*Thamnodynastes longicaudus* Franco, Ferreira, Marques & Sazima 2003

*Thamnodynastes cf. nattereri* (Mikan 1828)

*Tomodon dorsatum* Duméril, Bibrón & Duméril 1854

*Tropidodryas serra* (Schlegel 1837)

*Tropidodryas striaticeps* (Cope 1869)

*Xenodon guentheri* Boulenger 1894

*Atractus trihedrurus* Amaral 1926

*Atractus zebrinus* (Jan 1862)

*Caaeteboia amarali* (Wettstein 1930)

*Calamodontophis ronaldoi* Franco, Cintra & Lema 2006

*Clelia hussami* Morato, Franco & Sanches 2003

*Coronelaps lepidus* (Reinhardt 1861)

*Xenodon newiedii* Günther 1863

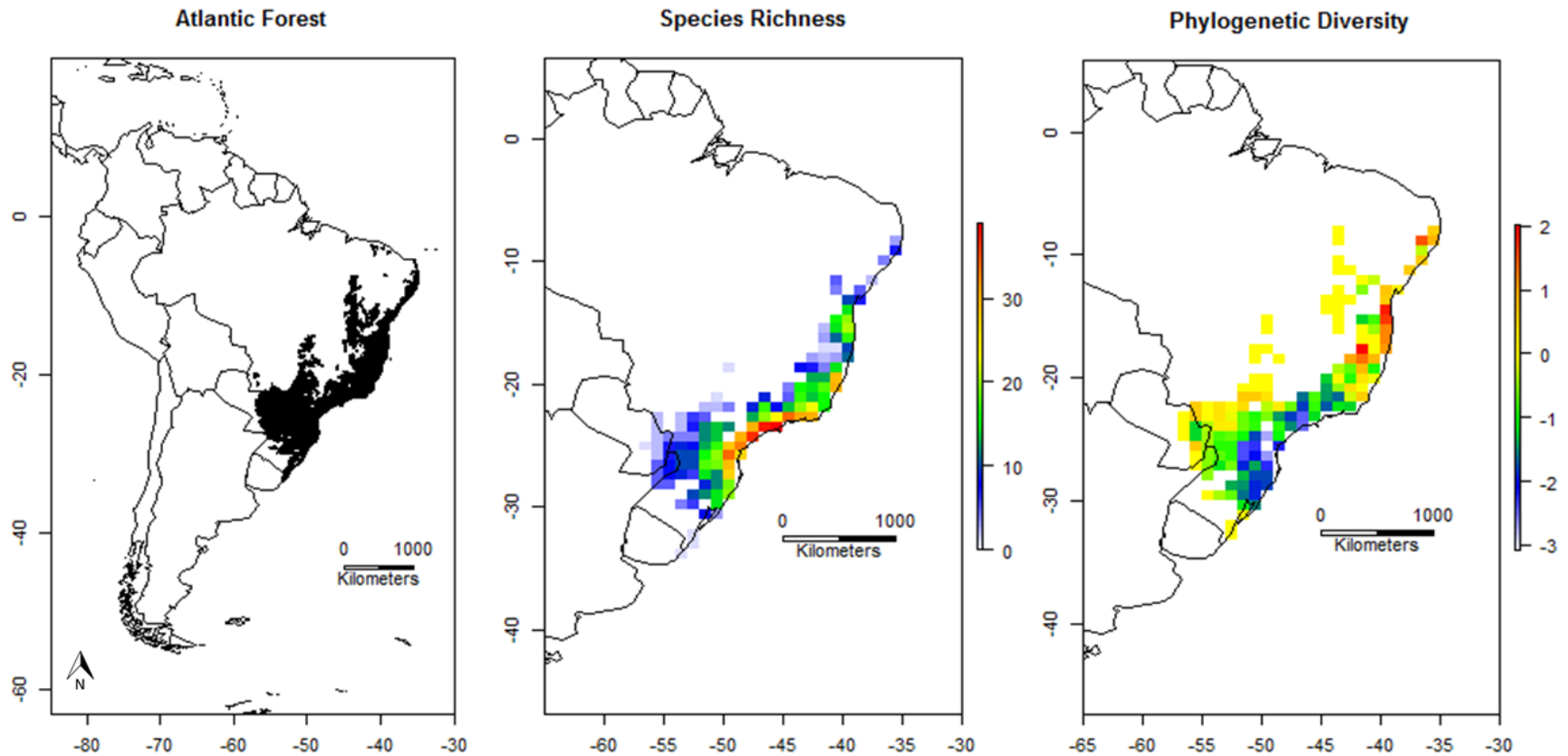
#### **Colubridae**

*Chironius foveatus* Bailey 1955

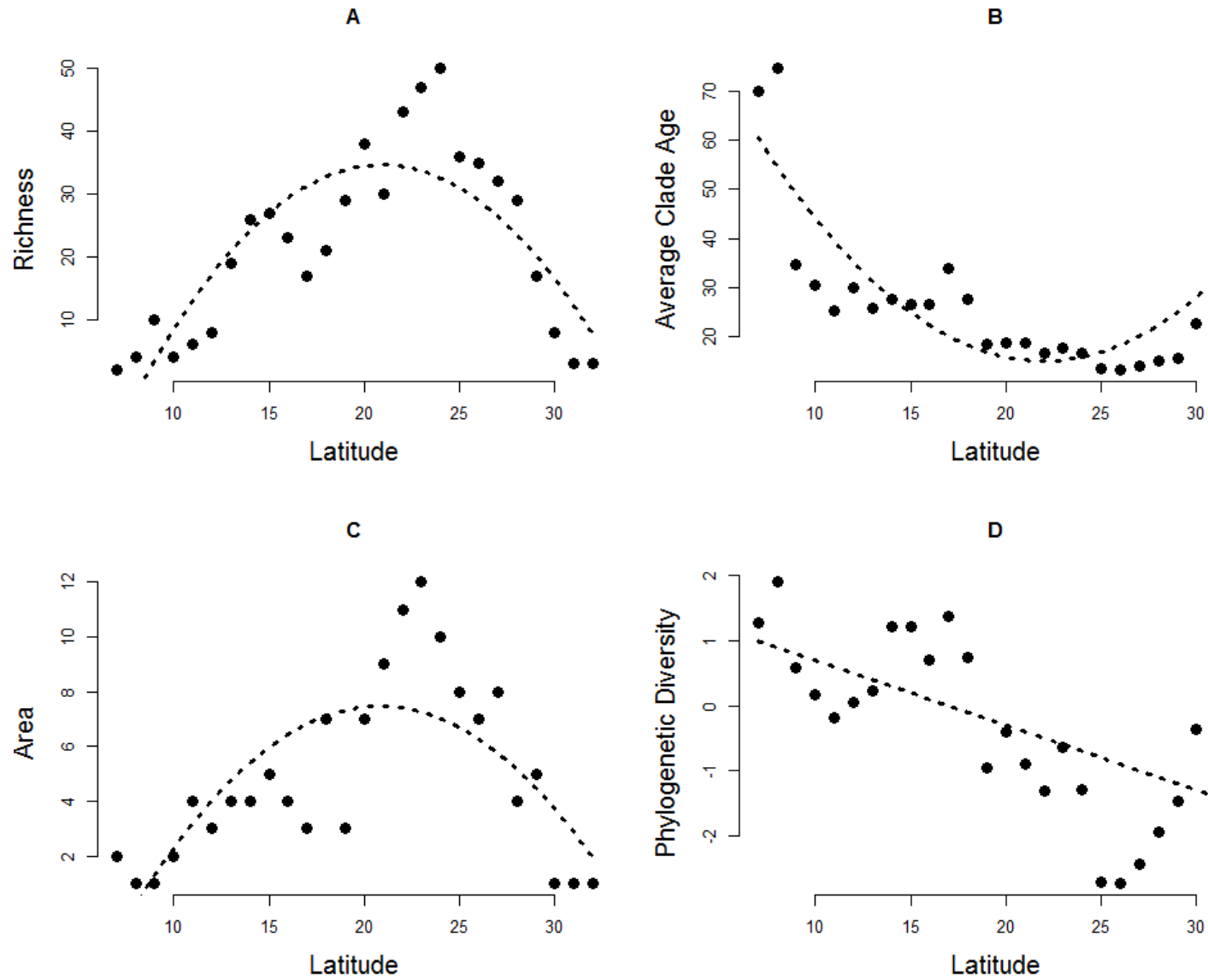
*Chironius laevicollis* (Wied 1824)

*Dendrophidion atlantica* Freire, Caramaschi & Gonçalves 2010





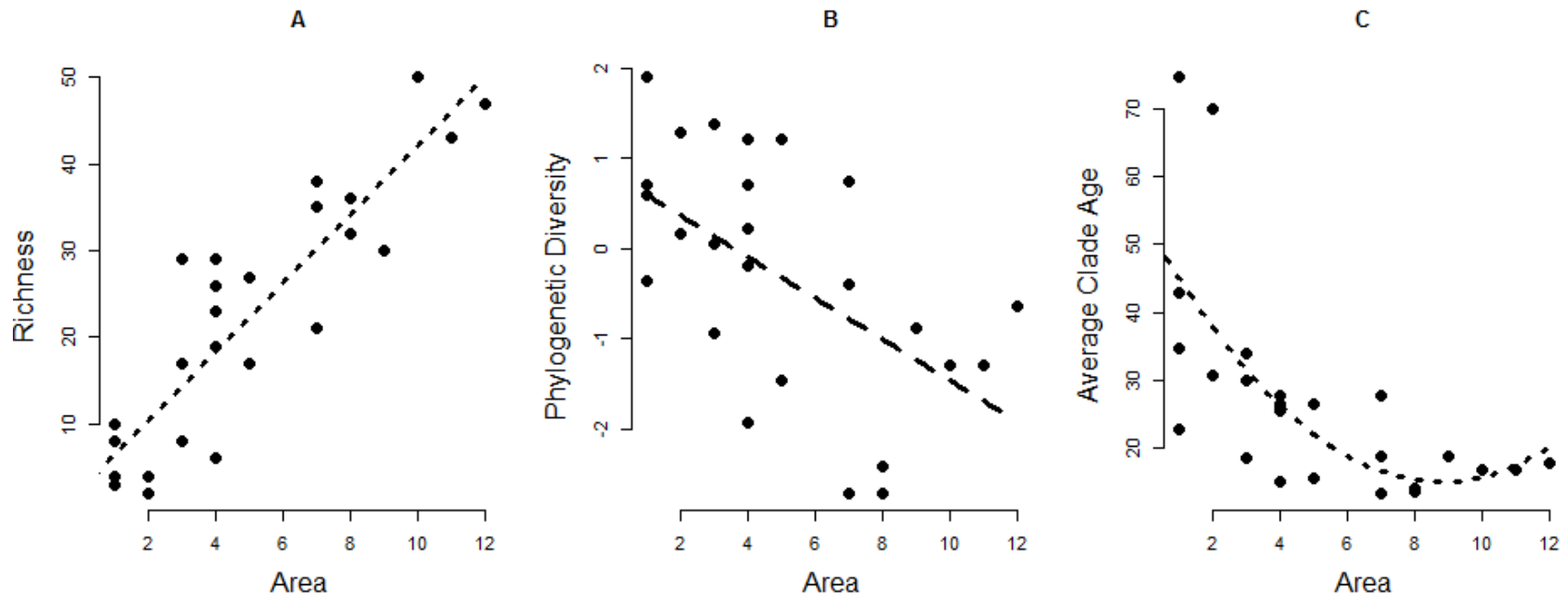
**Figure 1:** The Atlantic Forest of South America (left). Species richness (center) and phylogenetic diversity (right) of endemic snakes from the Atlantic Forest in 1 degree resolution. Species richness presents higher values in the southeastern region, with maximum value of 39 species per grid, highlighting the coastal mountain ranges. Lower values of phylogenetic diversity are located in areas with more recent lineages (see details in text and Fig. 2).



**Figure 2:** Latitudinal gradient of snake species richness (A) fitted by a quadratic model with highest values between 22 and 24 latitude south ( $R^2 = 0.67$ ;  $p < 0.01$ ). Average clade age (B) had an inverse relationship with species richness, also fitted by a quadratic model ( $R^2 = 0.66$ ,  $p < 0.01$ ). Area in square degrees (C) followed the species richness, with greatest geographical extent between 21 to 24 latitude south ( $R^2 = 0.51$ ,  $p < 0.01$ ). Phylogenetic diversity (D) of snakes was partially explained by a linear model with higher values generally in lower latitudes ( $R^2 = 0.30$ ;  $p < 0.01$ ). Dashed lines correspond to fitted models.

Area had a strong relationship with species richness, explaining 78% of the variation of species number for endemic snakes throughout the Atlantic Forest ( $p < 0.01$ , Fig. 3A). In contrast, decreasing phylogenetic diversity was associated to increasing area ( $R^2 = 0.31$ ,  $p < 0.01$ , Fig. 3B). Increasing area was negatively associated to average clade age across the latitudinal gradient (Fig. 3C;  $R^2 = 0.44$ ,  $p < 0.01$  for the quadratic model).

12



**Figure 3:** Relationships between area (square degrees) and species richness (A;  $R^2 = 0.78$ ,  $p < 0.01$ ), phylogenetic diversity (B;  $R^2 = 0.31$ ,  $p < 0.01$ ), and average clade age (C;  $R^2 = 0.44$ ,  $p < 0.01$ ) in Atlantic Forest endemic snakes.

## DISCUSSION

The distribution of endemism is strongly affected by climatic variation along the Atlantic Forest (Carnaval et al., 2014). Phylogenetic structure is variable across the latitudinal gradient of the Atlantic Forest (Moura et al., 2017). Northern areas show overdispersed phylogenetic structure, with more distinct lineages of snakes. Southern portions, on the other hand, have a clustered phylogenetic structure, with more proximally related species (Moura et al., 2017). An important gap in this context is the age of such clades. Variations in species richness and phylogenetic diversity along environmental gradients are expected to be related to clade age across space (Stephens & Wiens, 2003; Wiens, Pyron & Moen, 2011).

The presence of older lineages should be one of the most important evolutionary factors generating higher number of species along latitudinal ranges (e.g. Wiens & Donoghue, 2004; Hawkins & DeVries, 2009; Pyron & Burbrink, 2009; Buckley et al., 2010; Stevens, 2011; Romdal, Araújo & Rahbek, 2013; Morinière et al., 2016). Surprisingly, in our results species richness of snakes was negatively associated to average clade age in the Atlantic Forest. However, the variation of phylogenetic diversity, with higher values in lower latitudes, corroborates the “tropical niche conservatism” hypothesis (see Fig. 1, and Wiens & Donoghue, 2004). Moreover, area explained species richness distribution (see Fig. 3), but not phylogenetic diversity of Atlantic Forest snakes.

Ecological factors can affect species diversity (Jenkins, Pimm & Joppa, 2013; Mannion et al., 2014), restricting clades to climatic zones associated to latitudinal variation (Wiens & Donoghue, 2004; Kozak & Wiens, 2007; Pyron & Burbrink, 2009). Climate regimes can determine “biogeographical affinities” of species groups in latitudinal ranges, limiting clade dispersion across such gradients (Harrison & Grace, 2007). Snakes could be largely influenced by ecological factors such as temperature, solar radiation, productivity, and resource availability (Morales-Castilla et al., 2011). However, different clades might respond in different ways to these factors across habitats (see Currie, 1991).

Higher environmental heterogeneity can promote rapid divergence among populations, as observed in tropical mountain regions (Janzen, 1967; MacArthur, 1972; Pyron et al., 2015). We found that endemic species richness is concentrated in coastal ranges of southeastern Atlantic Forest, especially along the “Serra do Mar” and “Serra da Bocaina” ranges. The latitudinal ranges with highest

values of species richness include these complex mountain ranges harboring many endemic species. These areas encompass the higher geographical extent in the Atlantic Forest latitudinal gradient, and are an important stronghold of ombrophilous dense forests (see also Olson et al., 2001), with high numbers of endemic snakes. However, species richness alone does not fully capture all processes driving snake diversity in the Atlantic Forest, and phylogenetic diversity provides additional clues on the drivers of endemic species distribution.

The Atlantic forest can be considered as a complex mosaic with different ecological constraints among different habitats (Ribeiro et al., 2011). Its northern portion could present phylogenetic relationships with Amazonian clades, which was already detected with data on mammals (Costa, 2003). If the “tropical niche conservatism” hypothesis (*sensu* Wiens & Donoghue, 2004) is prevalent, the northern fauna should present higher average clade age, as we show here for snakes. The relative age of clades influences phylogenetic diversity values throughout the Atlantic Forest snakes. Furthermore, the presence of younger and phylogenetically clustered clades suggest that southeastern mountain ranges act as a current cradle of snake diversity in the Atlantic Forest (Moura et al., 2017).

The prevalence of recent clades in the larger portions of the Atlantic Forest is probably a result of higher diversification rates in regions where area is not a limiting factor. The trend of snake specialization regarding habitat use, including the restriction to forested areas and microhabitats (see Cadle & Greene, 1993; Greene & Greene, 1997), could result in reduced faunal interchange with adjacent non forested areas. Species distribution patterns are the result of the evolutionary history and ecological affinities of their ancestors (Wiens, 2004; Wiens & Graham, 2005; Losos, 2008; Pyron & Burbrink, 2009; Cooper, Jetz & Freckleton, 2010; Rivadeneira et al., 2011; Peterson, 2011; Giehl & Jarenkow, 2012; Ulrich et al., 2012; Romdal, Araújo & Rahbek, 2013; Kerckhoff, Moriarty & Weiser, 2014; Pyron et al., 2015). Thus, phylogenetic niche conservatism might favor geographical restrictions of a given clade to ancestral latitudinal ranges (see also Wiens & Donoghue, 2004; Pyron & Burbrink, 2009) and to particular habitats, which could explain the patterns found here.

## CONCLUSIONS

Higher average clade age was not related to species richness along the Atlantic Forest latitudinal gradient. Species richness was positively related to area, a possible result of higher carrying capacity and resource availability (Holt, 1993). Larger areas could also reduce stochastic extinctions (Kadmon & Allouche, 2007). Thus, area effect should be considered the most significant driver of species richness in the Atlantic Forest snakes. Furthermore, the “tropical niche conservatism” can explain the presence of many different lineages in lower latitudes, but not the number of species, indicating that clade history and age is also an important factor in understanding current biodiversity distribution.

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