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CAMPUS DE SÃO JOSÉ DO RIO PRETO

Biogeography and Ecophylogenetics of Atlantic Forest Snakes

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DOUTORADO

PÓS GRADUAÇÃO
EM BIOLOGIA ANIMAL

UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
Câmpus de São José do Rio Preto

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Biogeography and Ecophylogenetics of Atlantic Forest Snakes

São José do Rio Preto

2019

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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Câmpus de São José do Rio Preto.

Financiadora: CAPES.

Orientador: Prof. Dr. Ricardo J. Sawaya

São José do Rio Preto

2019

P852b

Portillo, José Thales da Motta

Biogeography and Ecophylogenetics of Atlantic Forest Snakes / José Thales da Motta Portillo. -- São José do Rio Preto, 2019

73 p.

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto

Orientador: Ricardo Jannini Sawaya

1. Biodiversidade. 2. Biogeografia. 3. Ecologia filogenética. 4. Mata Atlântica. 5. Serpentes. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto. Dados fornecidos pelo autor(a).

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25 de março de 2019

AGRADECIMENTOS

- Agradeço especialmente à minha família, meus pais Maria Silvia Vieira da Motta, José Antônio Portillo Guerrero, minha irmã Maíra da Motta Portillo e luz de pequeno Davi. Sem vocês não conseguiria... Muito obrigado!
- Agradeço a minha tia Maria e meu primo Arthur que sempre abriram as portas de casa para minhas investidas em São Paulo. Obrigado pela força!
- Obrigado à bondade de todos os guias espirituais, em especial à venerável Geshe Kelsang Gyatso Rinpoche, pela grande compaixão e excelsa sabedoria. Em especial, agradeço aos Professores de Dharma: Samira, Kelsang Janglam, Kelsang Nyangdê e Luíz Gabriel. Também agradeço a todos da Sangha do Centro Budista Jangchub Ling, especialmente a diretora administrativa Natália pelo grande esforço, exemplo de conduta e por todas as oportunidades.
- Agradeço aqui com poucas palavras, mas ampla gratidão, ao amigo e orientador Prof. Dr. Ricardo J. Sawaya. Obrigado pela paciência e amplos ensinamentos. Sou muito grato por todas as oportunidades!
- Um obrigado especial ao grande amigo Leo Malagoli que me ajudou muito no início do doutorado.
- Agradeço aos amigos Francisco Luis Franco, Marcelo Ribeiro Duarte e Waldir Germano pelas oportunidades, exemplo de conduta e incentivo no início da carreira.
- Obrigado a Thiago Gonçalvez Souza e Décio Tadeu Corrêa Filho pelos importantes ensinamentos no início do projeto e ampla ajuda em minha formação.
- Obrigado aos amigos Leandro da Silva Duarte, Lilian Sayuri Ouchi de Melo, Lucas Batista Crivellari e Thiago Alves Lopes de Oliveira. Agradeço pela grande ajuda em

meu aprendizado e, especialmente, pela paciência frente minhas limitações. Agradeço, especialmente, à Lilian pelas rápidas respostas e grandes ajudas.

- Obrigado a Fausto Erritto Barbo pelo auxílio na construção dos bancos de dados e pela grande ajuda sempre.
- Agradeço aos colaboradores do projeto "Atlas de Serpentes da América do Sul" (http://cnbiogeo.wixsite.com/cristiano-nogueira/atlas) que proveram registros revisados de distribuição de espécies de serpentes da Mata Atlântica.
- Obrigado aos Professores Dr. Fábio Sarubbi Raposo do Amaral e Dr. Cristiano de Campos Nogueira pela importante ajuda durante a primeira fase de minha qualificação.
- Obrigado a Dr. Cristiano Campos Nogueira pela ajuda na revisão do idioma.
- Obrigado ao Prof. Dr. Júlio Cesar Voltolini pela oportunidade de estágio docência na Universidade de Taubaté. Também agradeço aos alunos do curso de Licenciatura em Ciências Biológicas da Unitau pela grande força durante o estágio docência e por seus exemplos de esforço na formação.
- Obrigado a Dr. Vanderlei Júlio Debastiani pela grande ajuda na programação da quarta sessão deste trabalho, com biogeografia de ilhas, no software R.
- Obrigado a todos os amigos da Unesp de São José do Rio Preto. Obrigado pela hospedagem, conversas e amizade.
- Obrigado aos amigos do Laboratório de Ecologia e Evolução da Unifesp.
- O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Código de financiamento 001. E a Fapesp: proc. 2014/23677-9, Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP). Muito Obrigado!

RESUMO

A Mata Atlântica da América do sul é um mosaico de diferentes fitofisionomias, relacionadas a pressões seletivas correspondentes a fatores ecológicos e evolutivos distintos, os quais regulam a distribuição da biodiversidade entre os habitats. Exploramos, neste trabalho, como a diversidade de serpentes é distribuída ao longo do gradiente latitudinal da Mata Atlântica. Primeiro analisamos a associação entre a riqueza em espécies e a diversidade filogenética de serpentes com tempo para especiação e extensão geográfica ao longo do gradiente latitudinal. Nós também exploramos as amplitudes de nicho climático destas serpentes. E, finalmente, decompusemos a composição filogenética de ilhas costeiras do sudeste da Mata Atlântica no intuito de entender como área e distância com o continente poderia afetar diferentes componentes da diversidade de serpentes. Encontramos que área é o principal fator relacionado com riqueza em espécies, independentemente do tempo para especiação. Observamos a maior riqueza em espécies em linhagens mais recentes nas zonas serranas do sudeste. Amplitudes de nicho climático, associadas à precipitação, mostraram conservação filogenética, afetando a distribuição dos clados mais recentes. Em nosso exemplo de ilhas, mostramos que distintos fatores ecológicos podem afetar riqueza em espécies e diversidade filogenética diferentemente. Desta maneira, fatores idiossincráticos poderiam gerar diferentes respostas em diferentes linhagens ao longo do gradiente latitudinal. Esperamos trazer novas elucidações para fatores ecológicos e históricos relacionados com a distribuição da diversidade de serpentes na região Neotropical. Tal conhecimento é importante para proteger as espécies remanescentes deste tão ameaçado *hotspot* da biodiversidade, a Mata Atlântica megadiversa da América do Sul.

Palavras-chave: Biodiversidade. Biogeografia. Ecologia filogenética. Mata Atlântica. Serpentes.

ABSTRACT

The Atlantic Forest of South America is a mosaic of different vegetation physiognomies corresponding to distinct evolutionary and ecological factors that drive biodiversity distribution. One of these factors is climatic variation. We explored herein how snake diversity, (measured as species richness and phylogenetic diversity) is distributed along the Atlantic Forest latitudinal gradient, taking area and time-for-speciation into account. We first analyzed the association of species richness and phylogenetic diversity with time-for-speciation and geographical extent along the latitudinal gradient. We also explored climatic niche breadths. And finally, we decomposed the phylogenetic composition across coastal islands in southeastern Atlantic Forest, to understand how island area and distance from the mainland drive different components of snake diversity. We found that area is a major driver of species richness, regardless of time-for-speciation. We observed higher species richness of more recent lineages in southeastern mountain ranges. Climatic niche breadths associated to precipitation showed phylogenetic conservatism, affecting the distribution of more recent clades. In our island case study, we show that distinct ecological factors can drive species richness and phylogenetic diversity differently. In this way, idiosyncratic factors generate different responses in different lineages across environmental gradients. We hope to shed some light on ecological and historical factors related with snake diversity in the Neotropical Region. Such knowledge is important to conserve this threatened biodiversity hotspot, the megadiverse Atlantic Forest of South America.

Keywords: Biodiversity. Biogeography. Ecophylogenetics. Atlantic Forest. Snakes.

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1 INTRODUCTION

Understanding factors regulating biodiversity distribution is one of the central challenges of ecology and biogeography (STEPHENS & WIENS, 2003). Biodiversity distribution across latitudes, for instance, with increased species richness toward the tropics, has been one of the most explored environmental gradients in broad spatial scales (MACARTHUR, 1972; GASTON, 2000; BROWN, 2014; KERKHOFF *et al.*, 2014). However, the number of species does not encompass all factors driving different dimensions of biological diversity distribution. Additional components of diversity, such as phylogenetic diversity, highlight how phylogenetic relationships and evolutionary time could affect species numbers across environmental gradients (WIENS & DONOGHUE, 2004; PYRON & BURBRINK, 2009; QIAN *et al.*, 2015).

Phylogenetic diversity, or the sum of branch lengths within a phylogenetic tree (e.g. FAITH, 1992), and time-for-speciation provide a deeper understanding of drivers of species richness in biological communities (STEPHENS & WIENS, 2003; WEBB *et al.*, 2002; CIANCIARUSO *et al.*, 2009; PAUSAS & VERDÚ, 2010). The distribution of diversity across different scales can be related to the age of clades (PIANKA, 1966; STEPHENS & WIENS, 2003; PONTARP & WIENS, 2017), with richer areas harboring older clades due to longer time-for-speciation, and consequently higher phylogenetic diversity (WIENS & DONOGHUE, 2004; PYRON & BURBRINK, 2009). This trend can be related to general biogeographical patterns such as the latitudinal gradient of species richness (WIENS & DONOGHUE, 2004; WIENS, 2012).

Species richness is also strongly affected by area (HORTAL *et al.*, 2009; PARENT, 2012). The larger the geographical extent, the more habitat diversity, and consequently more species could co-occur (HORTAL *et al.*, 2009). The geographical limits for species occurrence are also determined by climatic niche breadths or, in other words, the interval of values between maximum and minimum temperature and precipitation in which a species can occur and persist (FISHER-REID *et al.*, 2012; SLATYER *et al.*, 2013; BONETTI & WIENS, 2014; CHEJANOVSKI & WIENS, 2014; ROLLAND & SALAMIN, 2016). Climate is the main ecological factor related to biodiversity constraints across environmental gradients (Qian et al. 2015), such as latitudinal variation on species richness (WIENS & DONOGHUE, 2004). Thus, species climatic niche breadths represent important constraints on biodiversity distribution across space (QUINTERO & WIENS, 2013).

Latitudinal gradient of species richness can be explained by the "Phylogenetic Niche Conservatism" (WIENS & DONOGHUE, 2004). It states that the area where ancestral lineages emerged, and subsequent geographical constraints on descendent lineages, can have a significant effect on species richness (WIENS & DONOGHUE, 2004; HAWKINS & DEVRIES, 2009; PYRON & BURBRINK, 2009; BUCKLEY *et al.*, 2010; RIVADENEIRA *et al.*, 2011; STEVENS, 2011; ROMDAL *et al.*, 2013; MORINIÈRE *et al.*, 2016). In this way, most clades could have tropical origins, generating the "tropical niche conservatism" pattern (*sensu* WIENS & DONOGHUE, 2004), based on the assumption that most clades had tropical origins and phylogenetic climatic niche conservatism would be prevalent. Thus, species richness and phylogenetic diversity would be higher near the region of their origin (the tropics), but also due to more area availability, longer time-for-speciation, and higher diversification rates in these areas (WIENS & DONOGHUE, 2004).

MOURA *et al.* (2017) state that snake phylogenetic structure varies across the latitudinal gradient in the Atlantic Forest. Northern areas show overdispersed phylogenetic structures, with more different lineages areas near the equator. On the other hand, a clustered phylogenetic structure emerges in southern coastal ranges, with fewer and closer lineages (MOURA *et al.*, 2017). Species richness would also be related to potential colonization, which might depend on area availability and isolation (PARENT, 2012). In this way, the classical Theory of Island Biogeography (MACARTHUR & WILSON, 1963; MACARTHUR & WILSON, 1967) would be an interesting model for understanding how phylogenetic composition (see DUARTE, 2011; DUARTE *et al.*, 2012) influences snake species richness and phylogenetic diversity. Each lineage should interact differently with environmental factors, such as area availability and distance from the mainland, and this diversity of interactions would regulate assembly processes in Atlantic Forest environments.

We analyzed herein ecological and evolutionary factors related to snake diversity distribution in the megadiverse Atlantic Forest of South America. Firstly, we tested the "Tropical Niche Conservatism" hypothesis (*sensu* WIENS & DONOGHUE, 2004) along the latitudinal gradient of species richness and phylogenetic diversity of snakes in the Atlantic Forest. We also explored the effects of latitudinal variation on climatic niche breadth of snakes. Finally, we assessed how phylogenetic composition is affected by ecological factors such as size and isolation on southeastern coastal islands of the Atlantic Forest. Besides contributing with novel data regarding the distribution of different components of snake

diversity throughout the Atlantic Forest, a megadiverse and extremely threatened Neotropical region, our work could contribute for a better comprehension of factors involved on assembly processes of snake communities in the Neotropics and in the globe.

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2 RICHNESS AND PHYLOGENETIC DIVERSITY ARE AFFECTED BY SPACE AND TIME IN THE MEGADIVERSE ATLANTIC FOREST OF SOUTH AMERICA

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2.1 ABSTRACT

Understanding variation of species richness along latitudinal gradients, with more species toward the tropics, represents a challenge for ecologists. Species richness can vary according to the available area, with more species in larger regions. Area and latitude are posited as important drivers of species number 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.

Keywords: Latitudinal gradient. Time-for-speciation. Species-area relationship. Atlantic Forest. Snakes.

2.2 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 are 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.

2.3 MATERIAL AND 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 analyzed the data and selected the endemic snakes of the Atlantic Forest region (*sensu* OLSON *et al*., 2001). We removed non entire values from the dataset. The raster files were transformed with values different of zero equal 1, and above 0.1 equal zero, maintaining all occurrence records into the dataset from binary maps. We maintained the one degree resolution into the data. We then summed raster files to calculate species richness of endemic snakes in the Atlantic Forest of South America.

Evolutionary relationships were obtained 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, based on the average age between the nodes from each phylogeny derived for each latitudinal range, of endemic lineages in each set of species from each latitudinal degree. Area was measured as the sum of

raster cells for 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).

2.4 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**	
Tropidophiidae	*Dipsas albifrons* (Sauvage 1884)
Tropidophis grapiuna (Curcio, Nunes, Argolo, Skuk & Rodrigues 2012)	*Dipsas alternans* (Fischer 1885)
Tropidophis paucisquamis (Müller 1901)	*Dipsas sazimai* Fernandes, Marques & Argolo 2010
Tropidophis preciosus (Curcio, Nunes, Argolo, Skuk & Rodrigues 2012)	*Echinanthera amoena* (Jan 1863)
Boidae	*Echinanthera cephalomaculata* Di-Bernardo 1994
Corallus cropanii (Hoge 1953)	*Echinanthera cephalostriata* Di-Bernardo 1996
Anomalepididae	*Echinanthera cyanopleura* (Cope 1885)
Liotyphlops caissara Centeno, Sawaya & Germano 2010	*Echinanthera melanostigma* (Wagler 1824)

Liotyphlops trefauti Freire, Caramaschi & Argolo 2007

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

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)

Echinanthera undulata (Wied 1824)

Elapomorphus quinquelineatus (Raddi 1820)

Elapomorphus wuchereri (Günther 1861)

Erythrolamprus atraventer (Dixon & Thomas 1985)

Helicops carinicaudus (Wied-Neuwied 1825)

Mussurana montana (Franco, Marques & Puorto 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

Xenodon neuwiedii Günther 1863

Colubridae

Chironius foveatus Bailey 1955

Chironius laevicollis (Wied 1824)

Dendrophidion atlantica Freire, Caramaschi & Gonçalves 2010

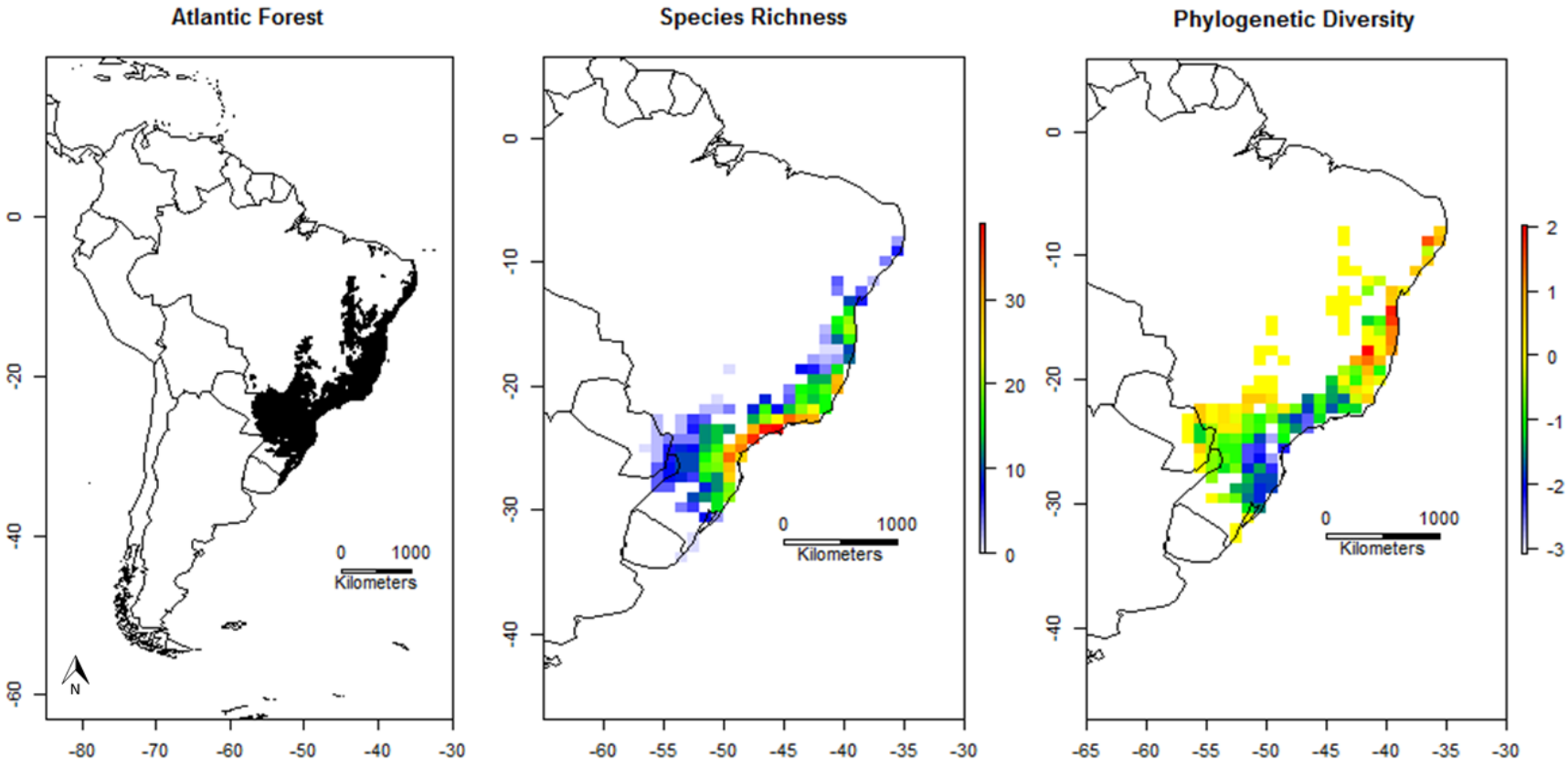

Figure 1: The Atlantic Forest of South America (left). Species richness (center) and phylogenetic diversity (right) of endemic snakes from the Atlantic Forest in 1 degree resolution. Species richness presents higher values in the southeastern region, with maximum value of 39 species per grid, highlighting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

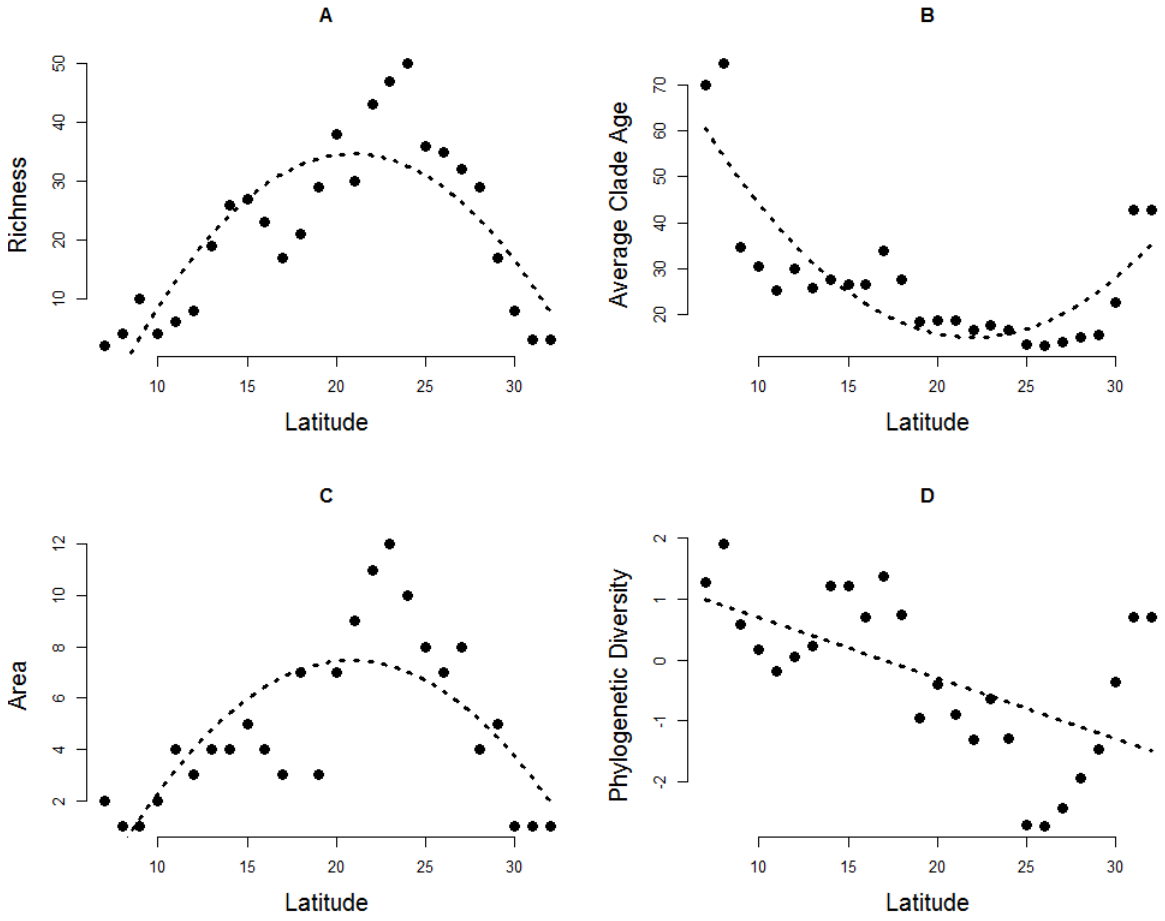

Figure 2: Latitudinal gradient of snake species richness (A) fitted by a quadratic model with highest values between 22 and 24 latitude south ($R^2 = 0.67$; $p < 0.01$). Average clade age (B) had an inverse relationship with species richness, also fitted by a quadratic model ($R^2 = 0.66$, $p < 0.01$). 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).

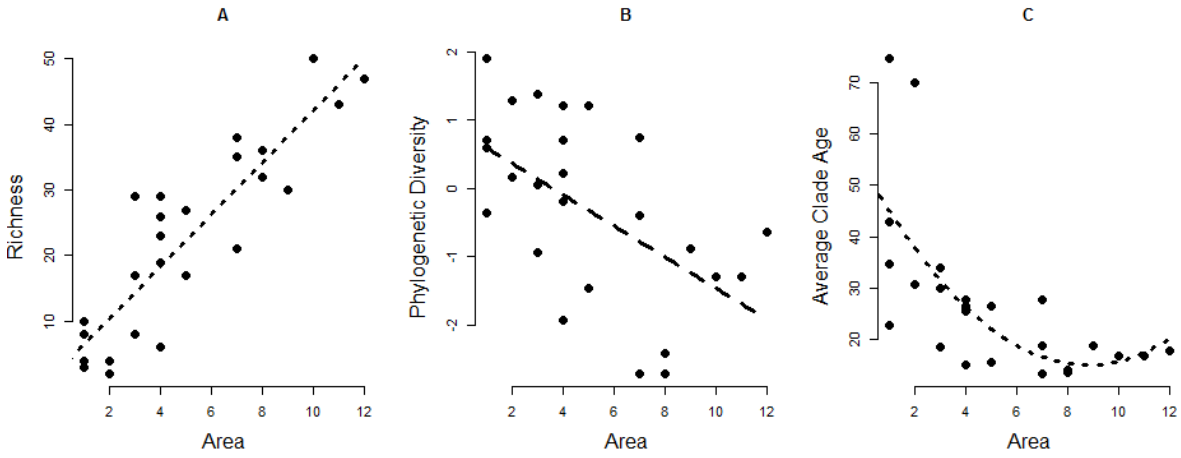

Figure 3: Relationships between area (square degrees) and species richness (A; $R^2 = 0.78$, $p < 0.01$), phylogenetic diversity (B; $R^2 = 0.31$, $p < 0.01$), and average clade age (C; $R^2 = 0.44$, $p < 0.01$) in Atlantic Forest endemic snakes.

2.5 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; KERKHOFF, 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.

2.6 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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3 CLIMATIC NICHE BREADTHS OF THE MEGADIVERSE ATLANTIC FOREST SNAKES DO NOT INCREASE WITH INCREASING LATITUDE

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3.1 ABSTRACT

The climatic niche is a central concept for understanding biodiversity distribution, with current and past climate interpreted as strong drivers of present and historical geographical ranges. This study aims to understand how snake climatic niche breadths are distributed along the Atlantic Forest latitudinal gradient, by testing two main hypotheses: the idea that niche breadth increases with increasing latitude, and the trade-off between temperature and precipitation niche breadths. We also assessed the phylogenetic niche conservatism of snake climatic breadths. Niche breadths were calculated via subtraction of maximal and minimal values of temperature and precipitation variables across species ranges. We used linear regressions to assess relationships between niche breadths and mean latitude on species ranges across the Atlantic Forest. We also implemented phylogenetic comparative methods and analyzed the phylogenetic signal of climatic breadths with Lambda statistic. We found that precipitation niche breadths decrease with increasing latitude. However, the high variance determined a low explanatory power within the latitudinal gradient analyzed. We then rejected both tested hypotheses. We found a significant phylogenetic conservatism for precipitation niche breadths and for geographical position from more recent clades. Our results show that precipitation is an important ecological influence for snake evolutionary history and can drive geographical distribution of younger lineages across the South American megadiverse Atlantic Forest.

Keywords: Biogeography. Latitudinal gradient. Climatic niche. Snakes. Atlantic Forest.

3.2 INTRODUCTION

Climate is the main ecological driver of species distribution constraints (QIAN *et al*., 2015). Geographical limits for species occurrence are determined by climatic niche breadths or, in other words, the interval between maximum and minimum values of temperature and precipitation in which species can occur and persist (FISHER-REID *et al*., 2012; SLATYER *et al*., 2013; BONETTI & WIENS, 2014; CHEJANOVSKI & WIENS, 2014; ROLLAND & SALAMIN, 2016).

Climatic conditions are also associated to species composition across environmental gradients, such as latitudinal variation of species richness on broad scales (WIENS & DONOGHUE, 2004). MACARTHUR (1972) suggest that niche breadths increase with increasing latitude and decreasing climatic stability, which could generate lower niche overlaps in tropical regions. Those factors consequently accelerate diversification processes in lower latitudes (MACARTHUR, 1972; see also KOZAK & WIENS, 2007; KOZAK & WIENS, 2010; FISHER-REID *et al*., 2012; SALISBURY *et al*., 2012; GÓMEZ-RODRÍGUEZ *et al*., 2015; ROLLAND & SALAMIN, 2016). In this way, latitudinal gradients show some trends of general biogeographical patterns associated with ecological and evolutionary factors (WIENS & DONOGHUE, 2004).

Temperature and precipitation niche breadths tend to be distinct along latitudes (VÁZQUEZ & STEVENS, 2004). There is actually a trade-off trend between temperature and precipitation conditions in broad scale latitudinal gradients. While temperature seasonal variation increases with latitude, the opposite occurs with precipitation (CURRIE, 1991; VÁZQUEZ & STEVENS, 2004). However, BONETTI & WIENS (2014) tested this trend and demonstrated that this trade-off is not applicable to amphibian's occurrence data, which show congruence between temperature and precipitation niche breadths along a latitudinal gradient. This example illustrates how empirical data can differ from general patterns as proposed by the MACARTHUR hypothesis (1972) or the environmental influence proposed by VÁZQUEZ & STEVENS (2004).

The Atlantic Forest of South America 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 198 species (MOURA *et al*., 2017), including at least 69 endemic snakes (GUEDES *et al*., 2018). And CARNAVAL *et al*. (2014) demonstrated that climate variation affects the geographic distribution of Atlantic Forest snakes. Lizards showed idiosyncratic responses to climatic factors with differential distribution of clades in this region (PRATES *et al*., 2016). But MOURA *et al*. (2017) argued that phylogenetic composition of snakes is strongly influenced by climate variations along the Atlantic Forest domain.

Different climatic regimes can determine habitat filters and different lineage composition throughout the Atlantic Forest ecoregions. And such variation can influence the regionalization of snake diversity not directly by latitude (MOURA *et al*., 2016, 2017). However, 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 & DONOGHUE, 2004; PYRON & BURBRINK, 2009; RIVADENEIRA *et al*., 2011; MORINIÈRE *et al*., 2016).

Phylogenetic niche conservatism, or the trend for each phylogenetic lineage to retain its adaptive traits across evolutionary history (HOLT & GOMULKIEWICZ, 2004; WIENS *et al*., 2010), 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 & VERDÚ, 2010; MOUQUET *et al*., 2012). It limits the adaptive responses to different environmental conditions and constrains dispersal rates across adjacent areas or latitudinal ranges (WIENS & DONOGHUE, 2004; PYRON *et al*., 2015). Thus, phylogenetic niche conservatism could restrict diversity along latitudinal gradients because of conserved climatic niche breadths in lineages adapted to climatic conditions in specific latitudinal ranges (WIENS & DONOGHUE, 2004; PYRON & BURBRINK, 2009; PYRON *et al*., 2015). Phylogenetic lineages can be restricting on latitudinal ranges where their ancestor emerged, presenting phylogenetic niche conservatism on geographical position and climatic conditions (WIENS & DONOGHUE, 2004).

We tested herein the hypothesis that climatic niche breadths increase with increasing latitudes using the Atlantic Forest snakes as a model. We also tested the proposed trade-off

between temperature and precipitation niche breadths. We implemented phylogenetic approaches to assess the phylogenetic niche conservatism for mean latitude of species occurrence, temperature and precipitation niche breadths. We then provide a general view of how lineages conserve their geographical position and the main ecological influences for the evolutionary history of snakes across the megadiverse Atlantic Forest of South America.

3.3 MATERIAL AND METHODS

3.3.1 *Species data*

We obtained presence records for each species from an expert verified database compiled by the project "Atlas of the South American snakes" (http://cnbiogeo.wixsite.com/cristiano-nogueira/atlas). Maps of 1 degree resolution of each species from those records are presented by GUEDES *et al*. (2018). We considered as the study area the delimitation of OLSON *et al*. (2001), but also including relictual forested areas within the Brazilian Caatinga and the Cerrado, based on IBGE ("Instituto Brasileiro de Geografia e Estatística", law number 11.428, dezember 2006) (Figure 1). Phylogenetic relationships of snake species were obtained in the consensus tree with 9755 species from TONINI *et al*. (2016).

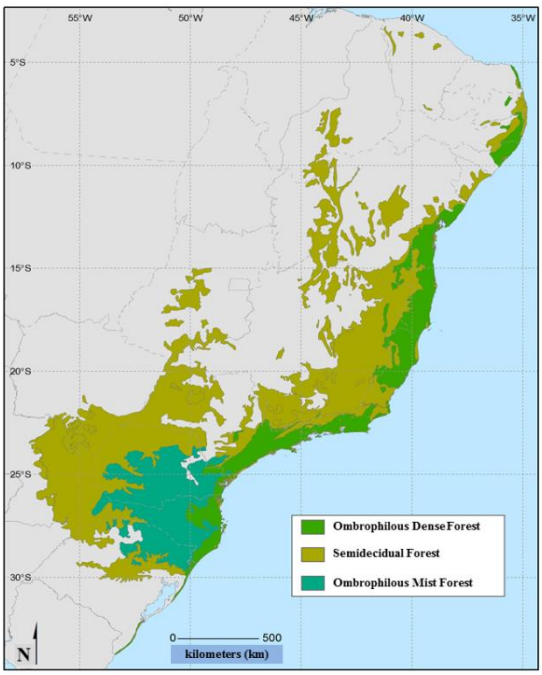

Figure 1: Study area with highlighted Atlantic Forest and their ecoregions according to OLSON *et al*. (2001) and "Instituto Brasileiro de Geografia e Estatística" (IBGE).

A total of 119.683 records of 199 snakes recorded in the Atlantic Forest were analyzed and species with peripherical distribution in the study area were excluded. For the remaining 150 species, we also removed species with less than ten records, including island endemic species, and missing species from the phylogeny. We then used the occurrence data for 126 snake species (see Appendix S1) recorded in the Atlantic Forest domain.

3.3.2 *Quantification of niche breadth*

We extracted bioclimatic values from Wordclim database (HIJMANS *et al*., 2005) for each occurrence of species records by *extract* function of *raster* R package (HIJMANS *et al*., 2015). Niche breadths were calculated by subtracting the minimum temperature of the coldest month (Bio6) from the maximum temperature of the warmest month (Bio5), and from wettest (Bio16) and driest (Bio 17) quarters of the year, using climatic variables of 30 seconds resolution (QUINTERO & WIENS, 2013). We then obtained temperature niche breadths and precipitation niche breadths for each snake species of the Atlantic Forest.

3.3.3 *Data analysis*

We used Phylogenetic Generalized Least Squares (PGLS - MARTINS & HANSEN, 1997) to analyze data (see also FELSENSTEIN, 1985; GARLAND & IVES, 2000; QUINTERO & WIENS, 2013). This phylogenetic comparative method identifies phylogenetic correlation on distribution of traits throughout environmental gradients, such as the distribution of climatic niche breadths across the Atlantic Forest latitudinal gradient (QUINTERO & WIENS, 2013). We complemented the analysis using Lambda statistic (PAGEL, 1992) to measure the degree of phylogenetic conservatism on geographical position (mean latitude of species range), temperature and precipitation niche breadths. The lambda values vary between 0, indicating no phylogenetic signal, to 1, or maximum phylogenetic signal of the analyzed trait. We also implemented linear regressions to assess latitudinal gradients of temperature and precipitation niche breadths, as well as to test the trade-off hypotheses between these predictors. All analyses were performed in R software (R CORE TEAM, 2018).

3.4 RESULTS

The PGLS analyses showed non-significant phylogenetic correlations for temperature and precipitation, with the same explanation power to lambda = 1 and lambda = 0. In this way, we did not find a phylogenetic correlation in climatic niche breadths within the latitudinal gradient of Atlantic Forest. Temperature niche breadths also did not show a significant relationship with latitude ($p > 0.01$). But precipitation niche breadths showed a significant negative relationship with latitude ($p < 0.01$; Figure 2). However, the high variance determined a low explanatory power ($R^2 = 0.18$).

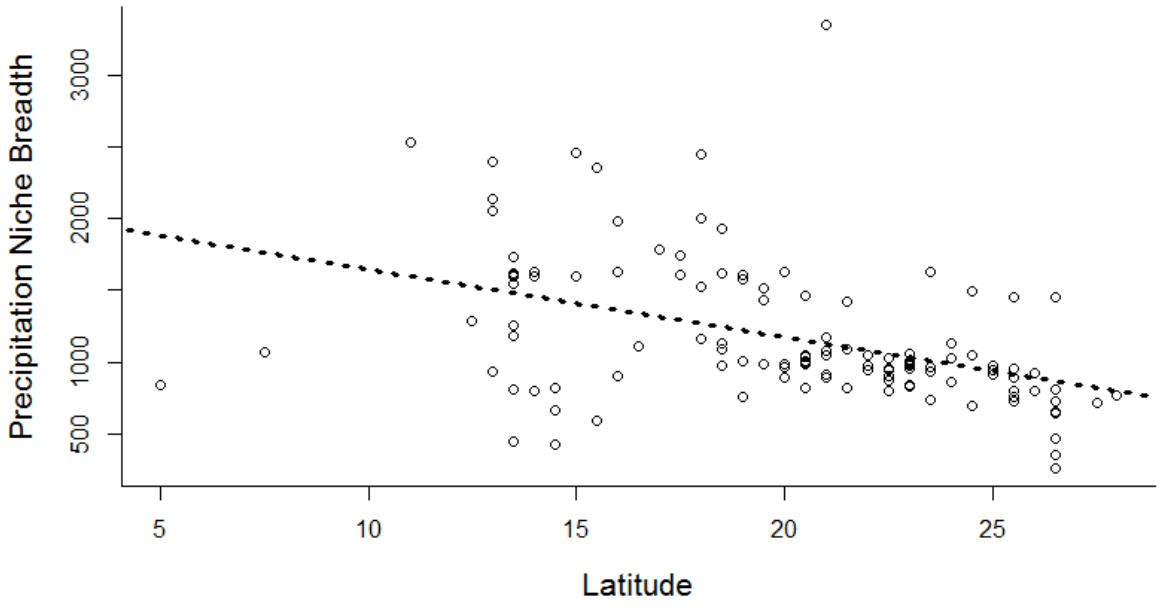

Figure 2: Linear model of precipitation niche breadths of Atlantic Forest snakes across the latitudinal gradient.

Temperature and precipitation niche breadths presented a non-significant relationship. The Lambda statistics indicated absence of phylogenetic signal on temperature niche breadths (lambda = 6.622063e-05; $p > 0.01$). But a significant phylogenetic signal was observed for precipitation niche breadths (lambda = 0.75; $p < 0.01$). Mean latitude of species ranges demonstrated a significant phylogenetic signal (lambda = 0.20; $p < 0.01$), but with a low lambda. This evidences that phylogenetic structure of geographical position is present for more recent lineages (see PAGEL, 1992). Our results indicate low influence of latitude on snake climatic niche breadths. We also detected significant phylogenetic niche conservatism

for precipitation and more related geographical position for younger lineages of Atlantic Forest snakes.

3.5 DISCUSSION

We conclude that latitude is not a good predictor for climatic niche breadths of snakes across the Atlantic Forest. Temperature and precipitation niche breadths were not correlated throughout the Atlantic Forest. And climatic niche breadths did not show a phylogenetic association with the latitudinal gradient. However, our phylogenetic signal analyses showed phylogenetic niche conservatism for precipitation niche breadth and for geographical position of more recent lineages. We then conclude that precipitation is an important ecological influence in the evolutionary history of Atlantic Forest snakes, and can drive geographical position of more recent clades.

We rejected the MACARTHUR (1972) hypothesis suggesting that climatic niche breadths increase in higher latitudes. In agreement with MacArthur hypothesis, JANZEN (1967) suggested that variation of climatic conditions influences species distribution. But this author highlights the importance of altitudinal gradients as a major determinant of diversity distribution. JANZEN (1967) proposes that climatic stability variation regulates the ability of a species to transpose adjacent areas with different climatic patterns. In other words, topographical barriers could be more significant in tropical regions because of greater climatic stability at lower latitudes (see too KOZAK & WIENS, 2007; KOZAK & WIENS, 2010; FISHER-REID *et al*., 2012; SALISBURY *et al*., 2012). However, our results showed that the decreasing of precipitation niche breadth with increasing latitude could also maintain these topographical influences in higher latitudes.

The climatic variation is regulated by physical and ecological factors such as topography and vegetation structure in the Atlantic Forest. Such factors are important ecological parameters explaining higher amphibian diversity on highly complex areas, such as the mountain ranges of southeastern Brazil (VASCONCELOS *et al*., 2014). The lower tolerances of climatic conditions could strengthen geographical barriers caused by topographical variation along complex tropical mountain ranges (see KOZAK & WIENS, 2007). Furthermore, these biogeographical barriers could favor reproductive isolation decreasing gene flow among populations and, consequently, promoting allopatric speciation

(KOZAK & WIENS, 2007; KOZAK & WIENS, 2010; FISHER-REID *et al*., 2012; SALISBURY *et al*., 2012; GÓMEZ-RODRÍGUEZ *et al*., 2015; ROLLAND & SALAMIN, 2016). Thus, precipitation and topography should be considered as important factors related to snake composition across the Atlantic Forest range.

MOURA *et al*. (2017) argued that thermal constraints regulate species composition and phylogenetic beta diversity in the Atlantic Forest. However, the differences in climatological regimes across this complex biome also regulate the species coexistence, which can be related with rainfall where the climatic niche partitioning is significant. In this way, biotic interactions and neutral processes can structure ectothermic assemblages in the Atlantic Forest hotspot (MOURA *et al*., 2017). We reinforce that this climatic niche partitioning is phylogenetic structured by precipitation regimes. And phylogenetic conservatism of latitudinal mean position evidenced herein that more recent lineages could be more affected by the climatic niche partitioning in the phylogenetic clustered assemblages from southern region, as indicated by MOURA *et al*. (2017). Our results are in line with findings of MOURA *et al*. (2017), demonstrating the phylogenetic niche conservatism of precipitation regimes in the Atlantic Forest of South America. However, the synergism of thermal and water conditions for tropical ectotherms (MOURA *et al*., 2017) was not confirmed herein. We just evidence phylogenetic niche conservatism for precipitation niche breadths, also strongly related with geographical position for more recent lineages.

The Atlantic Forest snake composition is influenced by the interplay of ecological and evolutionary factors (MOURA *et al*., 2017). The phylogenetic signal analyses indicate that interactions between ecological and evolutionary factors are spatially more evident in younger lineages of snakes. KOZAK & WIENS (2010) showed that diversification rates among clades are highly related to climatic niche evolution and are associated with geographical isolation of taxa. The snake assemblages can be strongly influenced by climate-based forest refugia (CARNAVAL *et al*., 2014). 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 divergence could provide better indicators of evolutionary constraints regarding climate preferences (see TERRIBILE *et al*., 2009).

The snake composition in the Atlantic Forest range is strongly affected by sub region variations (MOURA *et al*., 2016), as we also demonstrated herein. The climatic variation demonstrates a simplest division of northern and southern climatic regimes associated with snake composition (see CARNAVAL *et al*., 2014; MOURA *et al*., 2016, 2017), with a great influence of topographic variation and snake physiological constraints (MOURA *et al*., 2016). We complemented herein the view of ecological (climate) and evolutionary time influences on snake composition across the Atlantic Forest (see also MOURA *et al*., 2016, 2017). Our results shed light for a major understanding of how climatic factors could be related to biogeography and evolution of the megadiverse snake fauna of the Atlantic Forest. Thus, integrative approaches of such factors are important for a better understanding of processes driving the biodiversity distribution in Neotropical region.

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3.7 APPENDIX S1

Table S1: List of 150 snake species with confirmed occurrence in Atlantic Forest. Species marked with an asterisk were excluded from analysis (see methods).

Species	N	Species	N	Species	N
Amerotyphlops brongersmianus	304	*Dendrophidion atlantica**	5	*Oxyrhopus guibei*	914
Amerotyphlops paucisquamus	13	*Dipsas albifrons*	100	*Oxyrhopus petolarius*	649
Apostolepis assimilis	359	*Dipsas alternans*	94	*Oxyrhopus rhombifer*	979
Apostolepis dimidiata	301	*Dipsas bucephala*	287	*Oxyrhopus trigeminus*	518
*Atractus caete**	2	*Dipsas catesbyi*	316	*Paraphimophis rusticus*	493
*Atractus francoi**	4	*Dipsas sazimai**	8	*Phalotris mertensi*	234
Atractus guentheri	19	*Dipsas variegata*	187	*Philodryas aestiva*	701
*Atractus maculatus**	5	*Drymarchon corais*	384	*Philodryas arnaldoi*	41
Atractus pantostictus	182	*Drymoluber dichrous*	265	*Philodryas laticeps**	6
Atractus paraguayensis	167	*Echinanthera amoena*	35	*Philodryas olfersii*	843
Atractus potschi	32	*Echinanthera cephalomaculata**	1	*Philodryas patagoniensis*	2057
Atractus reticulatus	389	*Echinanthera cephalostriata*	116	*Pseudoboa haasi*	187
Atractus ronnie	10	*Echinanthera cyanopleura*	199	*Pseudoboa nigra*	706
Atractus serranus	21	*Echinanthera melanostigma*	48	*Pseudoboa serrana*	38
Atractus trihedrurus	42	*Echinanthera undulata*	243	*Ptychophis flavovirgatus*	70
Atractus zebrinus	45	*Elapomorphus quinquelineatus*	186	*Rhachidelus brazili*	212
Boa constrictor	751	*Elapomorphus wuchereri*	55	*Sibon nebulata**	95
Boiruna maculata	717	*Epicrates cenchria*	316	*Sibynomorphus mikanii*	404
*Bothrops alcatraz**	1	*Erythrolamprus aesculapii*	532	*Sibynomorphus neuwiedi*	446
Bothrops alternatus	1543	*Erythrolamprus almadensis*	436	*Sibynomorphus ventrimaculatus*	374
Bothrops bilineata	279	*Erythrolamprus atraventer*	14	*Simophis rhinostoma*	319
Bothrops cotiara	128	*Erythrolamprus frenatus*	120	*Siphlophis compressus*	252
Bothrops diporus	861	*Erythrolamprus jaegeri*	765	*Siphlophis leucocephalus*	29
Bothrops fonsecai	85	*Erythrolamprus miliaris*	818	*Siphlophis longicaudatus*	84

*Bothrops insularis**	1	*Erythrolamprus poecilogyrus*	2031	*Siphlophis pulcher*	109
Bothrops jararaca	1267	*Erythrolamprus reginae*	692	*Sordellina punctata*	73
Bothrops jararacussu	449	*Erythrolamprus typhlus*	354	*Spilotes pullatus*	813
Bothrops leucurus	238	*Helicops carinicaudus*	194	*Spilotes sulphureus*	196
*Bothrops muriciensis**	1	*Helicops infrataeniatus*	526	*Taeniophallus affinis*	173
Bothrops neuwiedi	292	*Helicops modestus*	188	*Taeniophallus bilineatus*	104
*Bothrops otavioi**	1	*Imantodes cenchoa*	480	*Taeniophallus occipitalis*	337
Bothrops pirajai	16	*Lachesis muta*	458	*Taeniophallus persimilis*	24
*Bothrops sazimai**	1	*Leptodeira annulata*	1159	*Tantilla melanocephala*	442
Caaeteboia amarali	13	*Leptophis ahaetulla*	698	*Thamnodynastes longicaudus*	13
*Calamodontophis ronaldoi**	2	*Liotyphlops beui*	147	*Thamnodynastes nattereri**	84
Cercophis auratus	70	*Liotyphlops caissara**	1	*Thamnodynastes pallidus*	94
Chironius bicarinatus	784	*Liotyphlops trefauti**	4	*Thamnodynastes strigatus*	224
Chironius carinatus	212	*Liotyphlops wilderi**	8	*Tomodon dorsatum*	620
Chironius exoletus	786	*Mastigodryas bifossatus*	1083	*Trilepida salgueiroi*	30
Chironius flavolineatus	487	*Micrurus altirostris*	866	*Tropidodryas serra*	100
Chironius foveatus	95	*Micrurus corallinus*	636	*Tropidodryas striaticeps*	212
Chironius fuscus	391	*Micrurus decoratus*	119	*Tropidophis grapiuna**	2
Chironius laevicollis	180	*Micrurus frontalis*	574	*Tropidophis paucisquamis*	14
Chironius quadricarinatus	469	*Micrurus ibiboboca*	66	*Tropidophis preciosus**	2
Clelia hussami	25	*Micrurus lemniscatus*	433	*Xenodon guentheri*	71
Clelia plumbea	418	*Micrurus potyguara**	3	*Xenodon merremii**	149 2
*Corallus cropanii**	4	*Mussurana montana*	18	*Xenodon neuwiedii*	527
Corallus hortulanus	439	*Oxybelis aeneus*	674	*Xenodon rabdocephalus*	186
Coronelaps lepidus	34	*Oxyrhopus clathratus*	592	*Xenopholis scalaris*	103
Crotalus durissus	1211	*Oxyrhopus formosus**	9	*Xenopholis undulatus*	68

4 AREA AND DISTANCE FROM MAINLAND AFFECT IN DIFFERENT WAYS RICHNESS AND PHYLOGENETIC DIVERSITY OF SNAKES IN ATLANTIC FOREST COASTAL ISLANDS

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4.1 ABSTRACT

The Theory of Island Biogeography posits that ecological and evolutionary processes regulate species richness of isolated areas. We assessed the influences of an island area and distance from the mainland on species richness, phylogenetic diversity and phylogenetic composition of snakes on coastal islands of the megadiverse Atlantic Forest in southeastern Brazil. We compiled the species composition of 17 coastal islands in southeastern Brazil. Species richness and phylogenetic diversity were calculated for each island. Phylogenetic composition was measured using principal coordinates of phylogenetic structure. We then employed generalized linear models to test the influence of area and distance from the mainland on the diversity metrics. We found a prominent influence of area on species richness, whereas phylogenetic diversity was more affected by distance from the mainland. Snake clades were

distinctly associated with area and distance. The Boidae family was associated with nearer and larger islands, whereas Elapidae was broadly distributed. Distance from the mainland was associated with the distribution of Dipsadidae, whereas Colubridae was influenced by both the area and distance. The Viperidae family attained higher values of phylogenetic diversity in smaller and more remote islands. This island system conserved a considerable piece of snake richness from southeastern Brazil, including island endemic species. Area and distance from the mainland were important drivers of snake diversity in the Atlantic Forest coastal islands. However, these predictors affected the different components of diversity in different ways. Phylogenetic composition analysis enables us to understand how basal nodes contributed to high levels of phylogenetic diversity on smaller and farther islands regardless of the decrease in species richness.

Keywords: Island biogeography. Species-area. Distance. Phylogenetic composition. Snakes. Atlantic Forest.

4.2 INTRODUCTION

MacArthur and Wilson's Theory of Island Biogeography proposes that ecological and evolutionary processes, such as colonization, speciation, and stochastic extinction, regulate species richness in isolated areas by creating an equilibrium between the gain and/or exclusion of species (MACARTHUR & WILSON, 1963; MACARTHUR & WILSON, 1967). The fundamental prediction of the Island Biogeography theory is that the rates of processes involved are dependent on the geographical context, whereas island area and isolation play significant roles in the species richness equilibrium (PATINO *et al*., 2017). Thus, species richness is expected to decrease in smaller islands farther from the mainland due to greater local extinctions and less immigration, and to increase in larger islands closer to the mainland because of the high levels of immigration and larger area available for foraging (MACARTHUR & WILSON, 1963; MACARTHUR & WILSON, 1967; WARREN *et al*., 2015). Larger islands also tend to hold larger populations by reducing the probability of stochastic extinctions (WHITTAKER & FERNÁNDEZ-PALACIOS, 2007).

Most studies testing predictions of the Theory of Island Biogeography have focused on species richness patterns (e.g., KADMON & PULLIAM, 1993; KALMAR & CURRIE, 2006; LINDGREN & COUSINS, 2017). As an example, Centeno, Sawaya & Marques (2008)

corroborated the Theory of Island Biogeography by comparing the structures (species richness, composition, and dominance) of snake assemblages in a Brazilian tropical island system, which suggested that relictual snake populations from the continental lowland and Serra do Mar coastal range were part of the island's composition. However, diversity on islands could also be related to evolutionary processes, such as the time available for speciation and rates of extinction in the regional species *pool* (LOSOS & SCHLUTER, 2000; RABOSKY & GLOR, 2010). Furthermore, strong evidence exists of fast speciation within islands (e.g., AMARAL, 1921; BARBO *et al*., 2012; BARBO *et al*., 2016), which contributes to the assembling process in the area, with endemic species being generated in some island systems.

LOMOLINO (2000) note some paradigms and limitations of Island Biogeography Theory, including spatial and temporal scales, immigration filters (e.g., intervening landscapes or seascapes and environmental conditions regarding island size), the neutral theory, and the challenge of evolutionary approaches to better clarify the assembly process in insular community structures. However, even the combination of molecular phylogenies and species composition has not been well explored to investigate the role of speciation in driving island community structures.

We have experienced an era of rapidly emerging community phylogenetic tools, making it feasible to test island biogeography predictions through an evolutionary timescale. Recently, PYRON & BURBRINK (2014) employed community phylogenetic tools to analyze patterns of snake diversity of 510 islands around the globe and demonstrated that colonization was the main process explaining most of species richness distribution patterns in islands. Furthermore, they verified *in situ* diversification as rare and not contributing to island species richness. These authors also have shown that phylogenetic diversity on islands is associated with isolation and climate but not area. Herein, we advance our understanding by identifying the influence of area and distance from the mainland on snake lineages in a megadiverse tropical biodiversity hotspot. We also shed light on the possible processes responsible for island community assembly under a phylogenetic approach.

We aimed to assess the accuracy of the predictions of the Theory of Island Biogeography for the determination of species richness, phylogenetic diversity and lineage composition of snakes among the coastal islands in the Atlantic Forest hotspot. We sought to answer the following questions: 1) Do species richness and phylogenetic diversity of coastal islands increase in larger and closer islands? and 2) How different are the phylogenetic

components regarding the variation in island area and distance from the mainland? We expected that species richness and phylogenetic diversity would present a positive relationship to area and a negative association to distance from the mainland, as predicted by Island Biogeography Theory, but different lineages should affect richness and phylogenetic diversity of snakes in islands differently.

4.3 MATERIAL AND METHODS

4.3.1 *Study area and database*

We analyzed 17 coastal islands located in the Atlantic Forest domain in São Paulo state, southeastern Brazil (23°23'00“ to 25°19'13“S and 44°43'44“ to 48°06'00“W). Precipitation in the islands ranges from 90 to 330 mm/year, and the average temperatures ranges from 18°C to 27°C (CICCHI *et al*., 2007). The climate is considered tropical by PEEL, FINLAYSON & MCMAHON (2007). These islands conserve dense ombrophilous forest and herbaceous shrub phytophysiognomies, as well as “restinga” vegetation (ROCHA *et al*., 2008; CICCHI *et al*., 2009; KURTZ *et al*., 2017).

The number of species was recorded from Cicchi *et al*. (2007), CENTENO, SAWAYA & MARQUES (2008), ROCHA *et al*. (2008), CICCHI *et al*. (2009), and BARBO *et al*. (2012). We considered, as a regional pool, 108 species with potential occurrence in the dense ombrophilous forests of the region (see ZAHER *et al*., 2011), which makes them potential colonizers for studied islands. To characterize island areas and distance from the mainland, we extracted data from CICCHI *et al*. (2007) (Table 1). We considered, as the local pool, the species composition of each island. In this way, we provided a complete list of the 40 species included in our analyses (Table 1 and Appendix S2).

4.3.2 *Phylogenetic diversity and composition*

To estimate phylogenetic diversity, we used a consensus phylogenetic tree from TONINI *et al*. (2016) encompassing 9755 species of Squamate reptiles. Missing species (*Echinanthera bilineata*, *Thamnodynastes nattereri* and *Xenodon merremii*) in this phylogeny were conservatively placed in polytomies within genera, along with their sister species, by

using the package phytools (REVELL, 2018) of R software version 3.2.1. *Bothrops otavioi* was manually moved in Mesquite Software (MADDISON & MADDISON, 2011), with the related island endemic species from the "jararaca" group (see BARBO *et al*., 2012) (Fig. 3).

We estimated phylogenetic diversity by using the richness-independent metric *Phylogenetic Species Variability* (PSV) (HELMUS *et al*., 2007). PSV quantifies the decrease in phylogenetic relatedness according to similarities shared by all species in a community (herein in each island), regardless of the total number of species. Briefly, PSV is an index based on the phylogenetic covariance expected for the related taxa, which is scaled between 0, where all species are closely related, and 1, where all species present a similar trend in the degree of relatedness, as with a star phylogeny (HELMUS & IVES, 2012). We used the package picante (KEMBEL *et al.*, 2018) to calculate the PSV index.

To evaluate the variation in lineage composition among islands, we used the principal coordinates of the phylogenetic structure analysis (PCPS; see DUARTE, 2011) calculated in the PCPS package (DEBASTIANI & DUARTE, 2014; DEBASTIANI, 2015). This approach allows verification of the main orthogonal gradient of the variation in the phylogenetic structure among the islands. The phylogenetic composition matrix was calculated using phylogenetic fuzzy weighting (see PILLAR & DUARTE, 2010; DUARTE *et al*., 2016) converted into a Bray Curtis dissimilarity matrix. The next step was to apply a principal coordinate analysis (PcoA) to generate principal coordinates of phylogenetic structure (PCPS) for each island. Each PCPS is a vector describing an orthogonal phylogenetic gradient of the lineages included (DUARTE, 2011; DUARTE, PRIETO & PILLAR, 2012). PCPS with higher eigenvalues depicts the monotonic gradient regarding basal nodes of the phylogenetic tree (DUARTE, PRIETO & PILLAR, 2012). As the PCPS eigenvalues decrease, finer phylogenetic gradients concerning more terminal nodes are described (DUARTE, PRIETO & PILLAR, 2012). Thus, to represent the phylogenetic composition, we selected the first two PCPS vectors with a significant association with predictor variables that represent the greater variation on phylogenetic composition structure regarding area and distance from the mainland.

4.3.3 Data analysis

We evaluated the collinearity among predictor variables with variance inflation factor analyses (VIF; ZUUR, IENO & ELPHICK, 2010), considering VIF < 3.0 as the threshold to exclude autocorrelated environmental predictors. After the VIF procedure, we standardized the predictors by scaling them to have the same range of variation (mean 0 and unit variance) to avoid potential type I and II errors.

To test the influence of island area and distance from the mainland on richness, phylogenetic diversity (PSV), and PCPS vectors, we used a generalized linear model (GLM) based on Akaike information criteria (AIC; BURNHAM & ANDERSON, 2002). The GLM model is a useful tool when the data exhibit nonconstant variance distribution or when no normal distribution of errors is present (CRAWLEY, 2007). GLM is able to define the type of error distribution by applying the best model to improve the correlation between the predictors and response variables, which is the Gaussian distribution in this case. We applied two different types of null models to access the significance of the GLMs: in the first one, the site positions were randomly shuffled across the environmental gradient; and, in the second, the species were randomly shuffled among the phylogeny tips, generating a set of 999 null PCPS (DEBASTIANI & DUARTE, 2014). All analyses were performed in R software 3.2.1 (R CORE TEAM, 2018).

We also tested spatial autocorrelation by Moran's I correlograms (LEGENDRE & LEGENDRE, 2012) for species richness, phylogenetic diversity (PSV index), and phylogenetic composition regarding PCPS vectors. Briefly, Moran's I is an index of similarity between values (herein all response variables) of two points, and such values of spatial autocorrelation are plotted as a function of distance classes on the abscissa (LEGENDRE & LEGENDRE, 2012). We chose a priori seven distance classes with equal number of sample units allocated in each class, which increases predictive power of the analysis (LEGENDRE & LEGENDRE, 2012). The significance test was based in 999 randomizations. We implemented Moran's I correlograms in the software *Spatial Analysis in Macroecology* (SAM; RANGEL *et al*., 2006, 2010).

4.4 RESULTS

We recorded 40 snake species belonging to five families on the 17 islands analyzed (see Appendix S2). The species pool of these islands represents approximately 37% of the regional pool (see ZAHER *et al*., 2011). The richest families were Dipsadidae and Colubridae, with 26 and seven species respectively. "Ilha do Cardoso" exhibited the highest species richness (25 species; Table 1), whereas "Ilhas dos Porcos" and "Ilha das Couves" showed the lowest species richness (only one species) and phylogenetic diversity (Table 1). The highest phylogenetic diversity was recorded in "Bom Abrigo" and "Queimada Grande" islands (both with PSV = 0.81) (Table 1).

Table 1: Coastal islands of the Atlantic Forest in southeastern Brazil and dataset of metrics used in this study. Predictor variables: area (hectares) and distance from mainland (kilometers) (from CICCHI *et al*., 2007); snake richness and phylogenetic diversity (*Phylogenetic Species Variability* - PSV); and assessed principal coordinates of phylogenetic structure (PCPS).

Islands	Area	Distance	Richness	PSV	PCPS 1	PCPS 3	PCPS 4
1-Alcatrazes	135	33.4	4	0.64	0.008	0.07	0.04
2-Anchieta	828	0.49	6	0.65	-0.13	-0.005	-0.05
3-Barnabé	173.4	0.01	2	0.59	0.2	0.06	-0.09
4-Bom Abrigo	154	3.55	2	0.81	-0.18	0.14	0.07
5-Búzios	755	24.09	4	0.68	-0.04	-0.02	-0.02
6-Cananeia	13.7	0.24	16	0.48	0.16	-0.04	0.002
7-Cardoso	22500	0.08	25	0.42	0.2	-0.02	-0.03
8-Comprida	20000	0.31	12	0.53	0.09	-0.07	-0.002
9-Couves	64.5	2.53	1	0.0	0.18	0.15	-0.15
10-Mar Virado	119	2	3	0.57	-0.18	-0.09	-0.15
11-Porchat	15	0.23	10	0.55	0.01	-0.07	-0.03
12-Porcos	24.2	0.74	1	0.0	-0.39	-0.21	-0.008
13-Queimada Grande	430	34.8	2	0.81	-0.21	0.15	0.07
14-Santo Amaro	14000	0.05	21	0.50	0.16	-0.07	0.17
15-São Sebastião	33600	1.76	22	0.49	0.17	-0.06	0.16
16-São Vicente	6000	0.12	22	0.44	0.19	-0.04	-0.02
17-Vitória	221.3	37.97	4	0.69	-0.24	0.13	0.05

We found that island area per se explained 53% of species richness variation (R^2 = 0.53, $p < 0.05$, Fig. 1A, Table 2). Our model was not improved by adding distance from the

mainland, as area and distance together explained the same 53% of species richness variation (p = 0.001, Table 2). Distance itself was not important in explaining species richness variation (p = 0.10). Area had a greater importance in driving species richness variation pattern in all evaluated models (wAIC = 0.74, Table 2). Regarding phylogenetic diversity, area explained 26% (p = 0.03), and the distance from the mainland explained 34% of the PSV variation (p = 0.01, Fig. 1B, Table 2). When considered together in the model, the area and distance explained 44% of the total PSV variation (p = 0.01, Table 2). Area and distance together presented the highest AIC weight (wAIC = 0.43, Table 2), but only distance from the mainland exhibited a great part of PSV explanation (wAIC = 0.40, Table 2).

Table 2: Influence of area and distance from the mainland on richness and phylogenetic diversity (PSV) of snakes recorded in the coastal islands of the Atlantic Forest in southeastern Brazil. Likelihood measures with Gaussian distribution. Abbreviations: AIC = Akaike information criterion; ΔAIC = Difference of Akaike information criterion to each model from the most parsimonious model; wAIC = AIC weight for each model; P = probability; and R^2 = adjusted coefficient of determination; Area = Island area in hectares; Dist = island distance from mainland in kilometers; Richness = number of species; and PSV = richness independent phylogenetic diversity (see methods for details). Significant relationships of metrics and correspondent predictors are denoted by *.

Model	**AIC**	**ΔAIC**	**wAIC**	**P**	**R^2**
Richness ~ Area*	114.3	0.0	0.74	0.0005	0.53
Richness ~ Dist	125.3	11	0.003	0.10	0.1
Richness ~ Area+Dist*	116.4	2.1	0.26	0.001	0.53
PSV ~ Area*	-19.5	1.9	0.17	0.03	0.26
PSV ~ Dist*	-21.3	0.2	0.40	0.01	0.34
PSV ~ Area+Dist*	-21.4	0.0	0.43	0.01	0.44

The first four principal coordinates of phylogenetic structure (PCPS) accounted for 59%, 27%, 17% and 13% of the total phylogenetic composition variation, respectively. The PCPS 1 had a significant relationship to area ($p_{site\ shuffle}$ = 0.05, Table 3). We did not find any relationship between PCPS 2 and the predictors. PCPS 3 was associated with distance from the mainland ($p_{site\ shuffle}$ = 0.02, Table 3), whereas PCPS 4 was significantly associated with

the island area ($p_{site\ shuffle}$ = 0.05; Table 3), as well as with the distance and area together ($p_{site\ shuffle}$ = 0.04; Table 3).

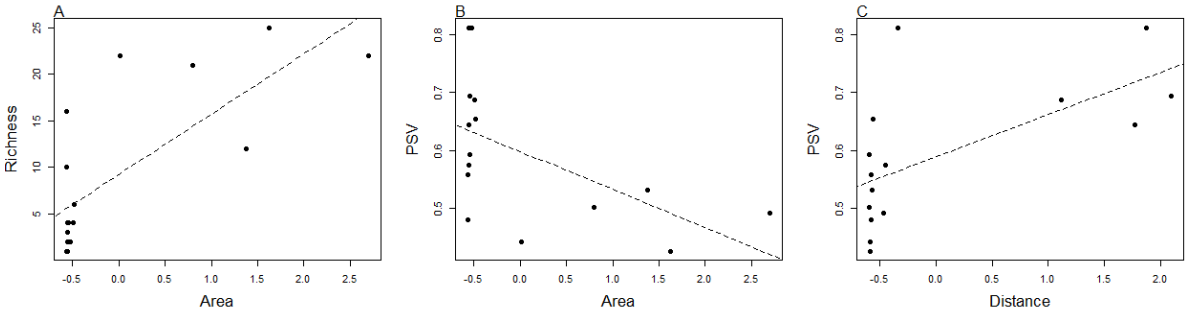


Figure 1: Relationships between island area (A and B) and distance from the mainland (C) on response species richness and phylogenetic diversity (*Phylogenetic Species Variability* – PSV; respectively). Species richness shows a significant positive association to area (R^2 = 0.53, p = 0.0005). Phylogenetic diversity presents a negative relationship with area (R^2 = 0.26, p = 0.03) and a positive relationship with distance from mainland (R^2 = 0.34, p = 0.01). See more details in Table 2.

Island area explained 18% of the variation in the phylogenetic composition (p = 0.05, Fig. 2A, Table 3) regarding PCPS 1 (basal nodes). On the other hand, distance from the mainland explained 25% of the variation in phylogenetic composition regarding PCPS 3 (p = 0.02, Fig. 2B, Table 3). Area and distance together explained 30% of the variation in phylogenetic composition among the islands (p = 0.03; Table 3) regarding PCPS 4. The area explained 16% of the phylogenetic composition variation regarding PCPS 4 (p = 0.05; Fig. 2C; Table 3).

Table 3: Environmental influence on phylogenetic composition of snakes (PCPS 1, PCPS 3 and PCPS 4) recorded in coastal islands of the Atlantic Forest in southeastern Brazil. Likelihood measures with Gaussian distribution. Abbreviations: AIC = Akaike information criterion; ΔAIC = Difference of Akaike information criterion from most parsimonious model; wAIC = AIC weight for each model; P = probability; and R^2 = adjusted coefficient of determination. Area = Island area in hectares, Dist = island distance from mainland (meters). Significant relationships of PCPS and correspondent predictors are denoted by *.

Model	f.obs	$P_{site\ shuffle}$	$P_{taxa\ shuffle}$	AIC	ΔAIC	wAIC	P	R^2
PCPS 1 ~ Area*	4.12	0.05	0.11	-5.7	0.0	0.52	0.05	0.18
PCPS 1 ~ Dist	2.52	0.13	0.3	-4.3	1.4	0.26	0.09	0.11
PCPS 1 ~ Area+Dist	2.68	0.09	0.21	-4.0	1.7	0.22	0.07	0.21
PCPS 3 ~ Area	2.25	0.15	0.36	-23.2	4.3	0.08	0.22	0.04
PCPS 3 ~ Dist*	7.5	0.02	0.05	-27.5	0.0	0.74	0.02	0.25
PCPS 3 ~ Area+Dist	4.11	0.04	0.12	-24.6	2.9	0.17	0.06	0.22
PCPS 4 ~ Area*	4.05	0.05	0.07	-30.7	0.6	0.4	0.05	0.16
PCPS 4 ~ Dist	1.08	0.34	0.4	-27.6	3.7	0.08	0.34	-0.002
PCPS 4 ~ Area+Dist*	4.5	0.04	0.05	-31.3	0.0	0.53	0.03	0.3

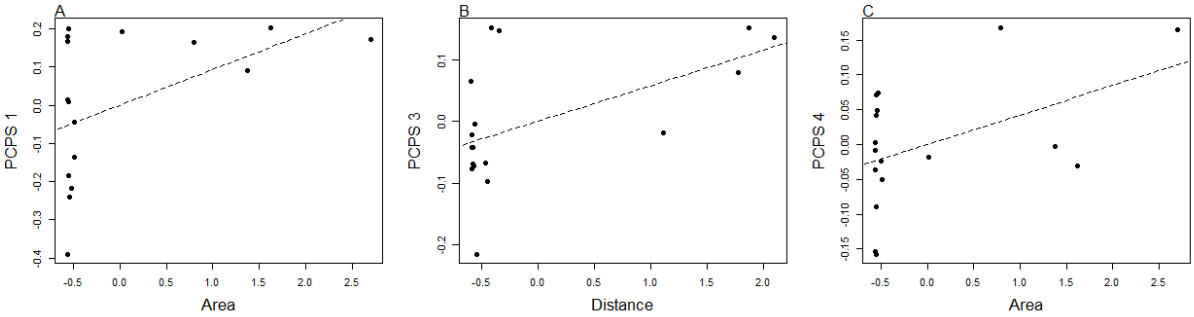
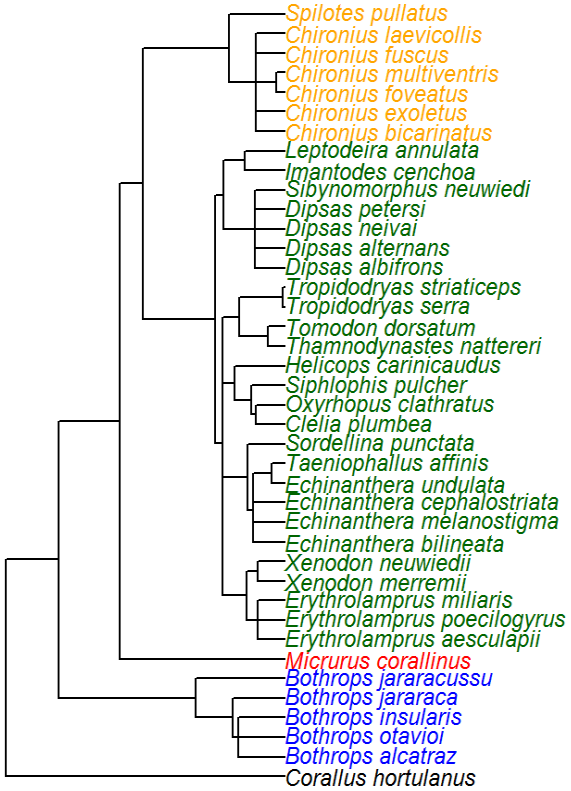
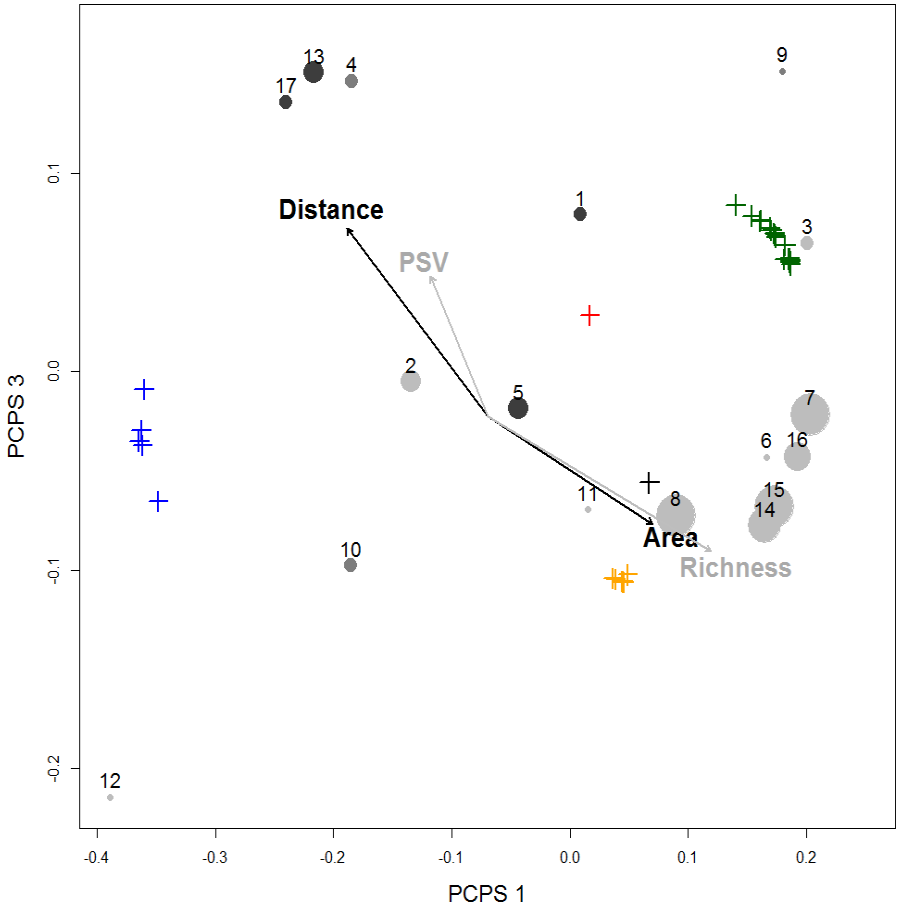


Figure 2: Relationships between principal coordinates of phylogenetic structure (PCPS) axes and predictor variables. A) PCPS 1 and area (R^2 = 0.18, p = 0.05); B) PCPS 3 and distance from mainland (R^2 = 0.25, p = 0.02); C) PCPS 4 and area (R^2 = 0.16, p = 0.05). See more details in the Table 3.

The ordination of the coastal islands and snake species along the PCPS 1 and PCPS 3 axes (Fig. 3) shows that species belonging to Boidae (*Corallus hortulanus*) and Colubridae families were associated with nearer and larger islands. The Elapidae family (*Micrurus corallinus*) was broadly distributed in coastal islands and does not show any significant association with the predictors. The Dipsadidae family presents a positive influence on species richness and phylogenetic diversity, whereas the Viperidae family species occur on small and more remote islands (Figure 3). Species richness, phylogenetic diversity (PSV index) and PCPS vectors did not present spatial autocorrelation (see Fig. S2 in Appendix S2).


Spilotes pullatus
Chironius laevicollis
Chironius fuscus
Chironius multiventris
Chironius foveatus
Chironius exoletus
Chironius bicarinatus
Leptodeira annulata
Imantodes cenchoa
Sibynomorphus neuwiedi
Dipsas petersi
Dipsas neivai
Dipsas alternans
Dipsas albifrons
Tropidodryas striaticeps
Tropidodryas serra
Tomodon dorsatum
Thamnodynastes nattereri
Helicops carinicaudus
Siphlophis pulcher
Oxyrhopus clathratus
Clelia plumbea
Sordellina punctata
Taeniophallus affinis
Echinanthera undulata
Echinanthera cephalostriata
Echinanthera melanostigma
Echinanthera bilineata
Xenodon neuwiedii
Xenodon merremii
Erythrolamprus miliaris
Erythrolamprus poecilogyrus
Erythrolamprus aesculapii
Micrurus corallinus
Bothrops jararacussu
Bothrops jararaca
Bothrops insularis
Bothrops otavioi
Bothrops alcatraz
Corallus hortulanus


Distance
PSV
Area
Richness
PCPS 1
PCPS 3
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
-0.2
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0.0
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Figure 3: Ordination of coastal island assemblages of Atlantic Forest in southeastern Brazil (circles), and snake families (crosses) along axis 1 and 3 of a principal coordinate analysis of phylogenetic structure (PCPS; see details in text). Numbers correspond to the islands listed in Table 1, and point sizes correspond to the total area of each island. Gray shades are related to distance from the mainland, with darker shades corresponding to greater distances. Correlations among environmental predictors and PCPS axes are highlighted by black vectors. Correlations among species richness and phylogenetic diversity (PSV) and PCPS axes are highlighted by gray vectors. Black cross is the score of Boidae family (*Corallus hortulanus*), blue crosses are scores of Viperidae family (*Bothrops* species), red cross is the score of Elapidae family (*Micrurus corallinus*), green crosses are scores of Dipsadidae family, and yellow crosses are scores of Colubridae family. All species are listed in the snake phylogeny in the left-hand side (modified from TONINI *et al*., 2016; see methods), with corresponding crossing colors in ordination.

4.5 DISCUSSION

The positive relationship between area and snake species richness follows Island Biogeography Theory predictions and matches our previous expectations, but we observed an idiosyncratic relationship of area and distance from the mainland for each diversity metrics analyzed. Phylogenetic diversity increases with distance from the mainland, independently of the decreasing richness, with regard to the phylogenetic structure distribution. More recent clades were clustered in the larger and nearer islands, whereas some older clades presented widespread distribution or defined greater phylogenetic diversity in more remote and smaller islands. Therefore, allopatric speciation events related to the occurrence of threatened endemic vipers in the Atlantic Forest island system (see BARBO *et al*., 2012, 2016) were an important factor in these differences among richness and phylogenetic diversity.

The species-area effect could be understood as a complementary view of habitat diversity as noted by HORTAL *et al*., (2009) for several animal groups, including vertebrates and invertebrates. These authors suggest that the size of the island environments leads to a monotonical increase in the available niche dimensions, and increasing habitat diversity should be related to an increase in species richness. Therefore, the maintenance of sink populations is also associated with the available species pool and, consequently, to habitat diversity (HORTAL *et al*., 2009). We reinforce the viewpoint that distance among assemblages and vegetation could be among the most important factors determining reptile

species composition in insular environments (see also GUERRERO, VARGAS & REAL, 2005). Thus, species richness would be related to potential colonization, which might depend on area and insularity (PARENT, 2012).

The relictual Atlantic Forest on islands conserves some lowland species from the southeastern coast and snakes of ombrophilous dense vegetation of Serra do Mar range (CENTENO, SAWAYA & MARQUES, 2008). Therefore, CICCHI *et al*. (2007) notes the fragility of these insular environments, where more than half of the snake species prey on amphibians, highlighting the importance of Forest conservation. Snake population survival and, consequently, the assemblage composition of the islands, tends to be affected by distinct mechanisms such as resource availability (primary productivity and prey availability), ecological conditions, habitat selection and environmental heterogeneity (HOLT, 1993).

Our results agree in part with those of PYRON & BURBRINK (2014), who, in their evaluation of island snakes on a global scale, found that phylogenetic diversity was related to isolation but not area. Herein, we found that area presented a negative relationship with phylogenetic diversity, whereas distance was positively associated to phylogenetic diversity variation, with greater weight, contradicting Island Biogeography Theory in terms of evolutionary diversity. PYRON & BURBRINK (2014) also used a richness-independent phylogenetic diversity metric (PSV) but did not explore how the different lineages were associated with the predictors of Island Biogeography Theory. Even with a greater number of species, the relatedness of species in the phylogeny, including more recent clades, corroborated the decrease in the phylogenetic diversity with increasing island area. In other words, larger islands presented phylogenetic clustered composition (see WEBB *et al*., 2002), which could indicate environmental filters defining species colonization of some specific traits (WEBB *et al*., 2002; GRAHAM *et al*., 2009, MOUQUET *et al*., 2012).

The phylogenetic clustered composition in larger islands should indicate more niche similarity among species and, consequently, the possibility of competitive exclusion effects (LOSOS, 1996; WEBB *et al*., 2002; PAUSAS & VERDÚ, 2010). However, the great fasting capability, annual seasonality of feeding resources, and variation in niche dimensions among species of snakes could prevent competition on populations and assemblages in this group (VITT, 1987). Therefore, we do not consider niche similarity as a factor generating competitive exclusion of closely related species, although food and substrate requirements might limit the distribution of taxa in these assemblages. However, the dispersion of individuals from the mainland to the islands or among insular populations could reduce the

extinction rates, given the proximity of this island system to the mainland (MACARTHUR & WILSON, 1963; BROWN & KODRIC-BROWN, 1977).

Most species within the coastal islands are a subsample of the mainland species pool, a situation that highlights the colonization effect as a very important driver of snake community assembly in island systems (BURBRINK *et al*., 2015). However, in our results, the increase on phylogenetic diversity was related to the occurrence of endemic species of Viperidae, which led to overdispersed assemblages in smaller and more remote islands (Figure 3), independent of the species richness reduction. Differently from BURBRINK *et al*. (2015), our results suggest the relevance of allopatric speciation to generate higher phylogenetic diversity and overdispersed assemblages in islands due to endemic *Bothrops* species on more remote islands. The maintenance of the basal clades (Viperidae) in this island system might maintain relatively longer branches among species on smaller and more remote islands, due to the occurrence of *Bothrops insularis, B. alcatraz* and *B. otavioi*, on the "Queimada Grande", "Alcatrazes", and "Vitória" islands, respectively. These endemic species are very important components of the phylogenetic diversity and fauna conservation of the southeastern Atlantic Forest islands.

Our results suggest that principal coordinates of phylogenetic structure provide a new interpretation of the environmental factors influencing phylogenetic lineages (DUARTE, 2011; DUARTE, PRIETO & PILLAR, 2012). The "phylogeny-weighted species composition" provides a way for us to indicate the relationships of each clade and environmental predictors as highlighted by DUARTE (2011). This author shows that species scores on PCPS ordination demonstrate the phylogenetic composition throughout the environmental gradient, while also indicating the clade distributions across environmental predictors. Moreover, we provide an additional view of the disparities of diversity metrics, including species richness and phylogenetic diversity, and how snakes respond to main predictors of the classical Island Biogeography Theory.

Island area showed a greater influence on Colubridae and the single Boidae species present. These species use arboreal substrates that, in turn, depend on the availability of forested habitat. The most diversified clade, Dipsadidae, includes terrestrial, arboreal and aquatic snakes and was also influenced by island area and mainland proximity, which would be related to habitat diversity and heterogeneity (see HORTAL *et al*., 2009). Association with particular habitats could drive the snake composition on islands (BURBRINK *et al*., 2015). Therefore, area and distance from the mainland significantly influences snake species richness

regarding to the Colubridae and Dipsadidae clades. However, decreasing area and increasing the distance from the mainland boosted the Viperidae clade, causing phylogenetic diversity maintenance, while also providing evidence of allopatric speciation in these coastal islands.

Snakes typically display high degrees of specialization in resource use (GREENE, 1997), and the extinction rate of island reptiles can be related to natural history traits, including habitat specialization (FOUFOPOULOS & IVES, 1999). Therefore, the plasticity in natural history traits and habitat use could generate a trend for greater abundances of birds in the Canary Archipelago as well as to more successful survival on islands (CARRASCAL *et al*., 2008). Such a trend could also explain the greater occurrence of *Bothrops* species in smaller and more remote islands. *Bothrops alcatraz*, for instance, can prey mostly on centipedes and lizards, whereas *B. insularis* presents an increased venom efficiency on birds, the preferred prey of larger individuals (see MARTINS *et al*., 2001; MARTINS, MARQUES & SAZIMA, 2002).

We corroborate the suggestion that the Brazilian southeastern islands maintain relictual snake populations of lowland species of Serra do Mar range (CENTENO, SAWAYA & MARQUES, 2008), which could be due to ecological plasticity and/or colonization success. We concluded that an island's area is more related to species richness, whereas distance from the mainland drives phylogenetic diversity on Atlantic Forest coastal islands. We empirically emphasize the importance of isolation to the evolutionary processes in driving phylogenetic diversity and lineage composition on island systems. The nearer and greater islands are very important to the maintenance of snake species richness, but we emphasize the need to conserve endemic species from isolated areas in the Atlantic Forest island system to preserve the snake phylogenetic diversity of this megadiverse domain.

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4.7 APPENDIX S2

Spatial autocorrelation is a common trend in biological data which could influence both the results and the interpretation of statistical analyses. We used Moran's I correlograms to verify if response data (species richness, phylogenetic diversity, PCPS1, PCPS3 and PCPS4) present spatial autocorrelation trends, in order to provide a more robust interpretation of results. We did not find any spatial autocorrelation in response data (see Figure S1 below). The absence of spatial autocorrelation means that the distribution of response data values is not influenced by the distance among islands. This means that the effects of distance from the mainland and island area in response variables are not influenced by the distance among islands.

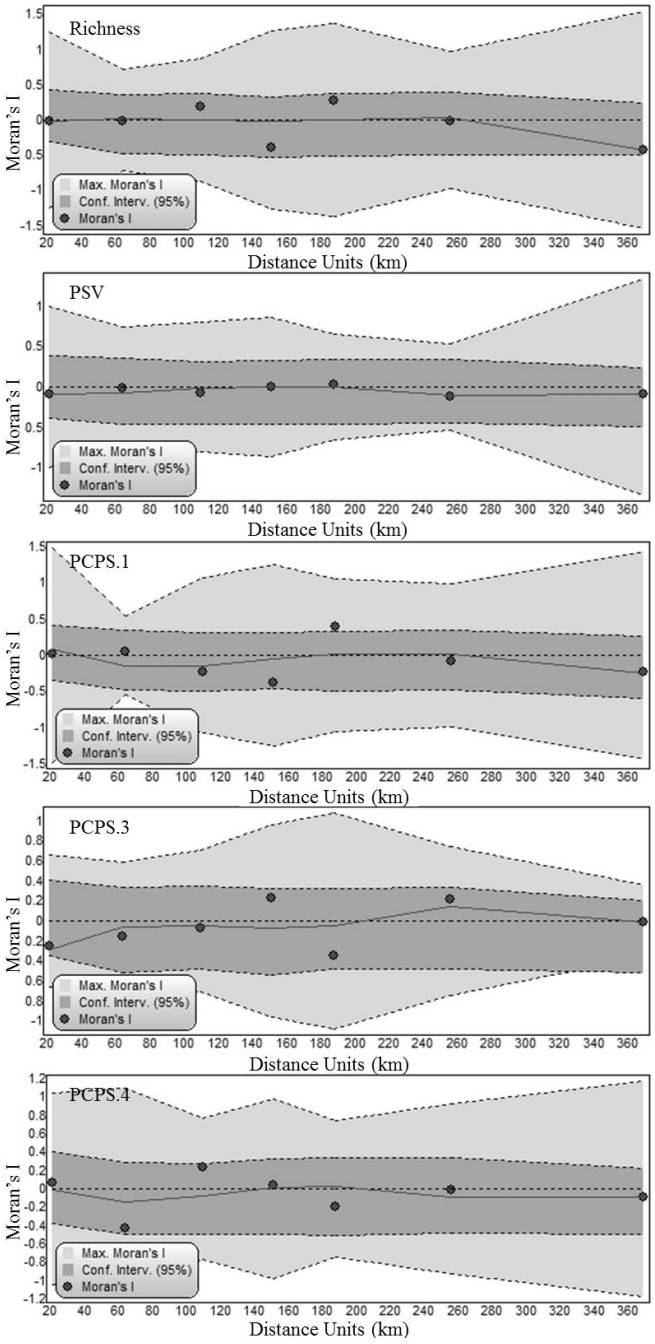

Figure S2: Moran's I Correlograms for species richness, phylogenetic diversity (PSV index; see methods), and phylogenetic composition regarding PCPS vectors of snakes from coastal islands in Atlantic Forest of southeastern Brazil. Values above zero represent positive autocorrelation and values below zero represent negative autocorrelation. Values inside the envelope of 95% confidence interval (darker shade) are non-significant.

Table S2: Occurrence of snake species in the coastal islands of the state of São Paulo, southeastern Brazil. The islands are numbered in alphabetical order: **1** = Alcatrazes, **2** = Anchieta, **3** = Barnabé, **4** = Bom Abrigo, **5** = Búzios, **6** = Cananeia, **7** = Cardoso, **8** = Comprida, **9** = Couves, **10** = Mar Virado, **11** = Porchat, **12** = Porcos, **13** = Queimada Grande, **14** = Santo Amaro, **15** = São Sebastião, **16** = São Vicente, and **17** = Vitória.

Family/species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Boidae																	
Corallus hortulanus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Colubridae																	
Chironius bicarinatus	0	1	0	0	1	1	1	1	0	1	1	0	0	1	1	1	0
Chironius exoletus	0	0	0	0	0	1	1	1	0	1	1	0	0	1	0	1	0
Chironius foveatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Chironius fuscus	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0
Chironius laevicollis	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Chironius multiventris	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0
Dipsadidae																	
Clelia plumbea	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Dipsas albifrons	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Dipsas alternans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dipsas petersi	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0
Dipsas neivai	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Taeniophallus affinis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Echinanthera bilineata	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Echinanthera cephalostriata	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0
Echinanthera melanostigma	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Echinanthera undulata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Erythrolamprus aesculapii	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0
Erythrolamprus miliaris	0	1	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1
Erythrolamprus poecilogyrus	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Helicops carinicaudus	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	1	0
Leptodeira annulata	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Imantodes cenchoa	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Oxyrhopus clathratus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0
Sibynomorphus neuwiedi	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0
Siphlophis pulcher	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0
Sordellina punctata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Spilotes pullatus	0	1	0	0	0	1	1	1	0	0	1	0	0	1	1	1	0
Thamnodynastes nattereri	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Tomodon dorsatus	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0
Tropidodryas serra	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Tropidodryas striaticeps	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Xenodon neuwiedii	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0
Xenodon merremii	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Elapidae																	
Micrurus corallinus	1	1	1	0	1	1	1	1	0	0	1	0	0	1	1	1	1

Viperidae																	
Bothrops alcatraz	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bothrops insularis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Bothrops jararaca	0	1	0	0	1	1	1	1	0	1	1	1	0	1	1	1	0
Bothrops jararacussu	0	1	0	1	0	1	1	1	0	0	1	0	0	1	1	1	1
Bothrops otavioi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

5 FINAL CONSIDERATIONS

5.1 FINAL REMARKS

Latitudinal gradients of biodiversity encompass ecological constraints and idiosyncratic processes related to the evolutionary history of distinct clades, generating biogeographical patterns of species richness and phylogenetic diversity (WIENS & DONOGHUE, 2004). We demonstrate herein that average clade age along the latitudinal gradient does not follow the expected pattern of more species with greater time-for-speciation. And the incongruence of species richness and phylogenetic diversity along the Atlantic Forest represents how complex are the Neotropical environments and biological assemblages.

The evolutionary history of clades interacts with different ecological constraints across habitats. The high number of specializations can also reduce the dispersal probabilities and increase local diversification rates for some clades (SALISBURY *et al.*, 2012). Furthermore, higher environmental heterogeneity can promote rapid divergence among populations (JANZEN, 1967; MACARTHUR, 1972; PYRON *et al.*, 2015), which would be the case in the Serra do Mar mountain range. But area effect is also significant, with a monotonic increase of species richness with area availability, regardless more time-for-speciation. Even with more time-for-speciation, older clades did not correlate with higher number of species in the Atlantic Forest as expected (see PIANKA, 1966; STEPHENS & WIENS, 2003; PONTARP & WIENS, 2017).

MANNION *et al.* (2014) and JENKINS *et al.* (2013) discuss that climatic niche breadths can regulate diversification rates. We assessed herein how ecological niche breadths of snakes vary across the latitudinal gradient. Reptile distribution along the Atlantic Forest in South America is regulated by distinct climatic factors in different habitat types (PRATES *et al.*, 2016; MOURA *et al.*, 2017). One intriguing aspect of diversity in the Atlantic Forest is that precipitation niche breadths are conserved across the evolutionary history of snakes, and more recent clades present evident phylogenetic niche conservatism. In this way, younger lineages can be more constrained by ecological factors, with great influence of topographical variation in mountain ranges of southeastern Atlantic Forest. Such evidence follows the idea from JANZEN (1967) that some topographic complex areas are more isolated on Tropical environments, which could favor allopatric speciation.

Snakes of the Atlantic Forest present narrow climatic niche breadths, which could generate less niche overlap and, consequently, accelerated diversification (MACARTHUR, 1972; KOZAK & WIENS, 2007, 2010; FISHER-REID *et al.*, 2012; SALISBURY *et al.*, 2012; GÓMEZ-RODRÍGUEZ *et al.*, 2015; ROLLAND & SALAMIN, 2016). More recent clades in complex mountain ranges can be more limited by ecological factors and thus unable to disperse to adjacent areas. Mountain ranges of southeastern Atlantic Forest conserve isolated ombrophilous forests with higher number of endemic species and phylogenetic niche conservatism, mainly influenced by precipitation.

Our case study with southeastern coastal islands demonstrates that different lineages are affected by distinct ecological constraints. Some clades are broadly distributed and some are restricted in some islands. Isolation can promote speciation, as observed for endemic island species (see BARBO *et al.*, 2012, 2016). Area availability was also a major ecological factor regulating species richness in Atlantic Forest coastal islands. These megadiverse areas conserve a mosaic of ecological and evolutionary factors, and can help us understand that general patterns can often neglect fine scaled processes in each particular habitat and clade. We provide herein novel data and interpretations on the megadiverse Atlantic Forest, and hope to shed some light on factors affecting the distribution of biodiversity in the Neotropical Region.

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