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Biogeography of snakes from the Gran Chaco

São José do Rio Preto
2023

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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.

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Orientador: Prof. Dr. Diego J. Santana
Coorientador: Dr. Pier Cacciali

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Dedico a meus pais, irmãos e sobrinhos,
sem eles nada disto seria possível

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I don't want to look back. I want to keep going forward, I still have something to say to people.

The future is unwritten.

(Joe Strummer)

RESUMO

Os estudos sobre a evolução e o padrão geográfico da biota Neotropical aumentaram rapidamente nas últimas décadas, com contribuições de quase todas as ecorregiões que abrangem uma variedade de organismos. No entanto, o conhecimento desses processos está centrado principalmente em florestas tropicais como a Amazônia e a Mata Atlântica, deixando de lado as áreas abertas da América do Sul, como Caatinga, Cerrado e Gran Chaco. No entanto, o Chaco é talvez o mais negligenciado desses três, com estudos que se concentram apenas na conservação, ou taxonomia de gêneros ou grupos específicos, ou não abrangendo toda a distribuição do Chaco, e só alguns tratando de processos evolutivos. Neste trabalho, usamos dados moleculares, ecológicos, morfológicos e de distribuição para estudar o processo evolutivo que moldou a distribuição de serpentes de áreas abertas, com ênfase principalmente no Chaco. Descobrimos que no Chaco, alguns caracteres evoluídos respondem a fatores bióticos e abióticos. Por exemplo, encontramos um padrão latitudinal, com uma acentuada verticalidade, na qual espécies fossoriais são impulsadas principalmente pelas condições do solo no Chaco. O padrão de distribuição das serpentes do Chaco também reflete sua história evolutiva, com uma marcada regionalização filogenética. Além disso, eventos no Mioceno/Plioceno como introgressões marinhas e oscilações climáticas, e a heterogeneidade da paisagem são importantes condutores da estrutura genética e história demográfica de *Erythrolamprus poecilogyrus caesius* no Chaco, do mesmo modo as introgressões marinhas e a formação da Bacia do Pantanal são importantes para explicar a diversificação e divisão de *Xenodon pulcher* e *X. matogrossensis*. Finalmente, espera-se que as assembleias de serpentes no Chaco mudem com os cenários climáticos no futuro próximo com uma clara tendência à homogeneização biótica da ecorregião, com consequente homogeneização da diversidade filogenética e funcional das assembleias locais. Essas mudanças negativas se refletiriam nas Unidades de Conservação do Chaco, das quais muitas UCs sofreriam homogeneização biótica e perda de riqueza de espécies.

Palavras–chave: Conservação. Distribuição. Ecologia. Evolução. Filogenia. Xenodontinae.

ABSTRACT

Studies on the evolution and geographical pattern of Neotropical biota has been increased rapidly in the last decades with contributions from almost all ecoregions covering a variety of organism. However, knowledge of these processes is mainly centered in tropical forests such Amazonia and Atlantic Forest, leaving aside the South American open areas, like the Caatinga, Cerrado and Gran Chaco. However, the Chaco is perhaps the most neglected of those three, with several studies that focus mainly on conservation, or taxonomy of specific genera or groups, or not covering the entire distribution of the Chaco, and just a few dealings with evolutionary processes. Here, we used molecular, ecological, morphological, and distributional to studies evolutionary process that shaped the distribution of snakes from open areas, with an emphasizing mainly on the Chaco. We found that in the Chaco, some characters evolved has a response to biotic and abiotic factors. For example, we found a latitudinal pattern, with a marked verticality, and fossoriality is mainly driven by soil conditions in the Chaco. The distribution pattern of Chacoan snakes also reflects their evolutionary history, with a marked phylogenetic regionalization. Also, events during Miocene/Pliocene like marine introgressions, climatic oscillations, and landscape heterogeneity are important drivers of the genetic structure and demographic history for *Erythrolamprus poecilogyrus caesius*, in the Chaco, and some marine introgresions and the formation of the Pantanal Basin are important in explain the diversification and split of *Xenodon pulcher* and *X. matogrossensis*. Finally, is expected that the snakes' assemblages in the Chaco change with climatic scenarios in a near future with clear trend to biotic homogenization of the ecoregion, with consequent homogenization of phylogenetic and functional diversity of local assemblages. These negative changes would be reflected in the Protected Areas of the Chaco, of which PAs would suffering biotic homogenization, and loss of species richness.

Keywords: Conservation. Distribution. Ecology. Evolution. Phylogeny. Xenodontinae.

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LIST OF ABBREVIATIONS

Mya	Millions of years ago
mtDNA	Mitochondrial Deoxyribonucleic Acid
bp	Base pair
ER	Equal rates
SYM	Symmetric rates
ARD	All rates different
MCMC	Markov chain Monte Carlo
pp	Posterior probability
HPD	Highest posterior density
ΔAICc	Delta Akaike Information Criteria with correction
wAICc	Weight Akaike Information Criteria
m.a.s.l	Meters above sea level
GARD	Global Assessment of Reptile Distributions
TT	Total length
TL	Tail length
SVL	Snout-vent length
mm	millimeters
VIF	Variance Influence Factor
AET	Annual actual evapotranspiration
NPP	Net primary productivity
NDVI	Normalized difference vegetation index
EVI	Enhaced Vegetation Index
TC	Tree cover
FRAG	Volumetric percentage of coarse fragments
SAND	Proportion of sand particles in the soil

km	Kilometers
PCA	Principal Component Analysis
SES	Standardized effect size
SAR	Spatial autoregressive models
ED	Evolutionary distinctness
NMDS	Non-metric multidimensional scaling
IIBP	Instituto de Investigación Biológica del Paraguay
LGE	Laboratorio de Genética Evolutiva
ZUFMS	Coleção Zoológica da Universidade Federal Mato Grosso do Sul
UFMS	Universidade Federal Mato Grosso do Sul
CA	California
USA	United States of America
PCR	Polymerase Chain Reaction
ASAP	Assemble species by automatic partitioning
GMYC	Generalized Mixed Yule Coalescent
BI	Bayesian Inference
IBD	Isolation by Distance
Hd	Haplotype diversity
AMOVA	Analysis of Molecular Variance
BSP	Bayesian Skyline Plots
FML	Fundación Miguel Lillo
MNHNP	Museo Nacional de Historia Natural del Paraguay
UNNEC	Universidad Nacional del Nordeste
IPCC	Intergovernmental Panel on Climate Change
SSP	Shared Socioeconomic Pathways
GCM	Generalized circulation models

ENM	Ecological niche models
RND	Random allocation of pseudo-absences
MXD	Maximum Entropy default
GLM	Generalized Linear Models
OBR	Occurrence-based restriction
PCoA	Principal Coordinate Analysis
UPGMA	Unweighted Pair Group Method with Arithmetic mean
PD	Phylogenetic diversity
PB	Phylogenetic beta diversity
SesMPD	Standardized effect size of mean pairwise distance
FRic	Functional richness
FEve	Functional evenness
FDis	Functional dispersion
PA	Protected Areas
WDPA	World Database Protected Areas

SUMMARY

1 INTRODUCTION

Studies on the evolution and geographical pattern of Neotropical biota have increased rapidly in the last decades with contributions from almost all ecoregions covering a variety of organism (BROWN et al., 2020; BRUSQUETTI et al., 2018; WERNECK, 2011; WERNECK et al., 2012). However, knowledge of these processes is mainly centered in tropical forests such Amazonia and Atlantic Forest, leaving aside the Dry Diagonal (VANZOLINI, 1963; WERNECK, 2011), which include the Caatinga, Cerrado and Gran Chaco (hereafter Chaco). Fortunately, in the last decade several studies aim to understand the evolutional and geographical pattern in open areas, with research on amphibians, mammals, fishes, and plants (AZEVEDO et al., 2021; CAMPS et al., 2018; DELSUC et al., 2012; FRANÇA et al., 2008; ROCHA et al., 2020; WERNECK et al., 2015).

The Chaco is perhaps the most neglected of those three, with several studies that focus mainly in conservation, or taxonomy of specific genera or groups, or not covering the entire distribution of the Chaco (ANDRADE-DÍAZ et al., 2019; NORI; GÓMEZ; LEYNAUD, 2011; SEMPER-PASCUAL et al., 2018), and just a few dealing with evolutionary process (BRUSQUETTI et al., 2019; CACCIALI et al., 2016a; DELSUC et al., 2012; NORI et al., 2016; ROMERO-MUÑOZ et al., 2020). In the case of reptiles, important works were published for the Cerrado (AZEVEDO; VALDUJO; NOGUEIRA, 2016; BARBO; NOGUEIRA; SAWAYA, 2021; NOGUEIRA et al., 2011) and Caatinga (CAMURUGI et al., 2022; GUEDES; SAWAYA; NOGUEIRA, 2014; WERNECK et al., 2015; XAVIER; GUEDES; NAPOLI, 2015).

In southern South America, one ecoregion with semiarid, stressful environments and marked climatic seasonality is the Great American Chaco, covering Argentina, Bolivia, Paraguay and Brazil (CABRERA, 1994; PRADO, 1993), one of the most extensive continuous forested areas of South America (BUCHER, 1982). The Chaco is the result of

Andean uplift, marine introgressions, and several alluvial systems (GREGORY-WODZICKI, 2000; HERNÁNDEZ et al., 2005; IRIONDO, 1993). The most important characteristic of the Chaco is his geomorphology, which consist in an extensive sedimentary alluvial plain with soils derived from the massive accumulation of Quaternary sediments (PENNINGTON; PRADO; PENDRY, 2000; PRADO, 1993). This region is characterized by xerophytic vegetation formed by a mosaic of grasslands, savannas, open woodlands, and thorn forest (PRADO, 1993; WILLIG et al., 2000). This area shows an impressive monotony along his distributions, with scarce high elevation hills, the few elevations hills are located mostly in their western limit in Argentina and Bolivia (PRADO, 1993), resulting in a horizontal terrain, provoking that only four allochthonous rivers crossing the Chaco (PRADO, 1993). So, apparently no geographical barriers for organism dispersion are present in the Chaco (BUCHER, 1982) nevertheless, some barriers have been proposed, like the Sierras Pampeanas and Subandinas in Argentina, and the rivers mentions above (IRIONDO, 1993).

In the Chaco, the highest absolute temperature for South America has been registered (PRADO, 1993), this area with maxima temperature up to of 48.9°C is referred by (PROHASKA, 1959) as the South American Pole of Heat. This extreme hot summer is associated with frost winters, in almost the entire Chaco, in some area's temperature can reach -1.1°C in Corrientes or -7.2°C, an east-west pattern (PRADO, 1993). The precipitation in the Chaco also follows an east-west gradient with more than 1200 mm of annual precipitation in the east to 350mm in the west (PRADO, 1993). This climatic condition is reflected in a marked dry and rainy season, in some west areas the summer rains are the only ones of the year (PRADO, 1993).

Among the Chaco, two regions could be differentiated, the Humid and Dry Chaco (DINERSTEIN et al., 2017). The Humid Chaco is characterized by a mosaic of gallery forest with flooded savannas with *Copernicia alba*, which that extends from east Bolivia to northern

Argentina, following the course of the Paraguay and in some parts the Parana River (PRADO, 1993), On the other hand, the Dry Chaco is characterized by xerophytic vegetation with thorny forest, from southwest Bolivia, west of Paraguay and northern Argentina (PRADO, 1993).

The first work that deals with the snakes of the Chaco is LEYNAUD & BUCHER (1999), which provides distributions maps, and natural history notes of the species known for the Chaco at that time. Subsequent works deals with the distribution, biology, or conservation of snakes from the Chaco of Argentina (ANDRADE-DÍAZ et al., 2019; GIRAUDO; SCROCCHI, 2002; GIRAUDO, 2002; LEYNAUD; BUCHER, 2005), Paraguay (CACCIALI et al., 2016b; CACCIALI; CABRAL; YANOSKY, 2015; CACCIALI; UBILLA, 2016), Bolivia (EMBERT, 2007; HARVEY, 1999; HARVEY et al., 2008; HARVEY; APARICIO; GONZALES, 2005; JANSEN; KÖHLER, 2008), and Brazil (SOUZA et al., 2010). Therefore, understanding the historical and evolutionary processes that have shaped the geographic pattern of species distribution in this region becomes increasingly relevant.

This become more important because, Chaco has been suffering high deforestation rates (HANSEN et al., 2013) and landscape degradation, making it a priority area for conservation (DE LA SANCHA et al., 2021; FRATE et al., 2015; KUEMMERLE et al., 2017). Several studies have pointed out the importance of taking conservation actions in the Chaco, along with measuring their threats and identifying priority conservation areas (KUEMMERLE et al., 2017; NORI et al., 2016; ROMERO-MUÑOZ et al., 2020; SEMPER-PASCUAL et al., 2018). However, most of those works was focused on mammals, birds, or amphibians. Recently, ANDRADE-DÍAZ et al. (2019) identified priority conservation areas for 12 endemic snakes of the Dry Chaco in Argentina. showing that expansion of the agricultural frontier has potentially negative effects on the distribution of snakes in this region, with deforestation being the biggest threat (ANDRADE-DÍAZ et al., 2019).

In this work, we aim to study the evolutionary process that shaped the distribution of snakes of the Dry Diagonal, with an emphasis mainly on snakes from the Chaco. In addition to the evolutionary process, we also are interested to fill the gap of knowledge of ecology, natural history, and conservation of the snakes inhabiting Chaco. Seen this, this contribution is divided into 4 chapters, the first one focus on the evolution of two discrete characters on the genus *Xenodon*, distributed along the forested and the dry diagonal of the Neotropics (Caatinga, Cerrado and Chaco). The second chapter is focused on the functional and evolutionary drivers that explain the geographic patterns of vertical stratification of snakes from the Chaco. Chapter three deals with the phylogeography of *E. poecilogyrus caesius*; and the diversification of *X. pulcher* and *X. matogrossensis* in the Chaco; finally, the fourth chapter focus on the conservation of snakes from the Chaco, in a future perspective.

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27 FINAL CONCLUSIONS

1. In *Xenodon* species with Batesian mimicry, and semi-fossorial habits with a preference for open areas, the rostral scale was modified as a shovel for burrowing. On the other hand, in species with terrestrial habits, their rostral scale remained rounded, probably due to the association for forested habitats. In conclusion, the evolution of the rostral scale in *Xenodon* may be related to abiotic factors, as an adaptation for open and forested habitats, and mimicry are related to the presence of venomous species like *Bothrops* or *Micrurus*, which through imitating them serve as a defensive strategy.
2. We present the first integrative approach that investigated macroecological and biogeographic patterns and the phylogenetic relationships of the Chacoan snakes, which represent a unique area. We found that as arboreality increases towards the north, fossoriality increases towards the south. The environmental pattern represents a marked vertical stratification in the Chaco, increasing as habitat heterogeneity increases. Fossoriality is strongly correlated with and thus driven by soil conditions. The distribution pattern in the Chaco is also explained by the evolutionary history of snakes in this region, with a marked phylogenetic regionalization.
3. As was reported in other research, marine introgressions, and the events occurring during Late Miocene and Pliocene/Pleistocene have shaped and were important drivers in the process of shaping the biota of southern South America, in this case snakes in the Chaco. However, the formation of the Pantanal has never been proposed as a driver of diversification for reptiles. We think that the evolution of fossorial habits related to abiotic

factors along with the events occurring during this period have influence the diversification process of *X. pulcher* in the Chaco and *X. matogrossensis* in the Pantanal. Nevertheless, we believe that with more data and other analysis we can have a better understanding of the evolutionary process of the Chaco and Pantanal. This represents the first integrative approach that evaluated and try to understand the evolutionary process that have shape and influence the distribution of snakes in the Chaco.

4. We found that snakes' assemblages in the Chaco would change with climatic scenarios in a near future (in the year of 2100), with clear trend to the biotic homogenization of the ecoregion. This biotic homogenization would be characterized by the replacement of less distributed species by widely distributed species, with consequent homogenization of phylogenetic and functional diversity of local assemblages. Also, it is likely that some species might be locally extinct, by losing their suitable habitat in the Chaco. Negative effects of biotic homogenization would be reflected in the phylogenetic diversity, because a reduction in the number of species, or less diverse assembles would make that the phylogenetic diversity in the entire area and between communities decrease. These negative changes would be reflected in the PAs of the Chaco, many PAs would suffering biotic homogenization, and loss of species richness.